

古生物誌丙種第五號

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英國裴爾森著

中國豬類化石

中華民國十七年九月

農林部地質調查所印行
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楊鍾健節要

本書所研究之材料，爲安迭生所採而儲存于伍捕殺拉者。其大半分均採自中國北方之三趾馬化石羣，但亦有少數自黃土，或自中國藥肆所得。

其採自黃土者，爲一種真正豬。而自三趾馬層中，則有三種最普通者爲一小而短幹動物，具有較原始之牙齒，而特殊之鼻與顳骨。此爲新屬，名曰 *Chleuastchoerus*。其他兩種則僅有一二牙床碎片爲其代表。一當爲“*Sus*”*erymanthus*(*Microstonyx*)其他爲“*Sus*”*hyotherioides*後者或可歸于皮格林氏(*Pilgrim*)之屬名 *Propotamochoerus*。至從藥肆所採得者，過於破碎，難得可靠之鑑定。其地質年代，尤不易確定。但無一不可歸於上述三趾馬群中三種之任一種者。此外或在地史較古時期，有一巨大低瘤牙式之屬曰 *Listriodon*，採自甘肅，此種與中中新世之 *Listriodon* 種極相近，但較爲進化。

茲將本書內所述各種列舉如下，詳須參照原文。

Listriodon gigas 新種

Chleuastchoerus stehlini 新屬種爲 Schlosser 所定。

“*Sus*” (*Microstonyx*) *erymanthus*? Roth & Wagner.

Propotamochoerus hyotherioides Schlosser.

Sus sp.

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Chinese Fossil Suidæ

BY

HELGA SHARPE PEARSON

University College, London

Plates I—IV and 37 figures in text



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INTRODUCTION.

THE MATERIAL DESCRIBED IN THIS PAPER IS PART OF THE *Lagrelius* collection made in China by Professor J. G. ANDERSSON, and housed in the Palæontological Institute of the University of Upsala.¹ With a generosity of which I am warmly appreciative, Professor C. WIMAN has sent me the Suidæ to study in England.²

The greater part of the material comes from the *Hipparion* fauna of Northern China. There are also fragments from the loess and even later deposits, and other fragments of uncertain origin, some of them bought in the Chinese medicine shops.

The remains from the loess are those of an ordinary modern species of *Sus*. From the *Hipparion* fauna come three types of Suidæ. The commonest of these is a small, gracefully proportioned animal with a rather primitive dentition but a peculiar snout and zygoma; this is clearly quite a new genus, and I have named it *Chleuastochærus*. The other two are large animals represented only by the fragmentary jaws of one or two individuals; one of these appears to be of the "*Sus*" *erymanthius* type (*Microstonyx* PILGRIM), the other of the species named by SCHLOSSER "*Sus*" *hyotherioides*; the latter is probably of the same genus as PILGRIM's *Propotamochærus*. The remains from the medicine shops are usually too fragmentary to be identified with confidence, especially as their geological age is uncertain, but there are none of them that might not belong to one of these three *Hipparion* fauna types. Probably from a yet earlier geological horizon are the fragments of a gigantic bunodont *Listriodon*, collected in a single locality in Kansu: these show affinity with the small bunodont *Listriodon* species of the European Lower and Middle Miocene, but differ in certain, probably progressive, characters.

¹ See recent monographs in the *Palæontologia Sinica* by RINGSTRÖM, ZDANSKY, and others.

² To Miss G. M. WOODWARD and Miss J. TOWNEND I am much indebted for their unsparing efforts to make strictly accurate those of the text figures which bear their names or initials. The plates are from photographs (touched up by the author) by Mr. JOHN THOMAS of the Zoological Department, University College London, and to him also I should like to express my thanks for the pains which he has taken with a difficult material.

I. LISTRIODON GIGAS sp. nov.

Locality: KANSU, Ping Fan Hsien, Chuan Tou Kou.

Definitive characters. Size gigantic, skeleton massive. Molars bunodont. M^3 with well developed talon, P^2 and p^3 with shallow basin-shaped talons. P_4 with, p_3 without deuterocoid. P_1 present.

The name *Listriodon* usually recalls the classical species of the European Middle Miocene, *Listriodon splendens* H. v. MEYER, with its specialised lophodont molar teeth. STEHLIN has shown,¹ however, that there also existed in Europe bunodont forms whose molar teeth had been previously confused with those of *Hyotherium* or *Sus*: he recommended a division of these forms into the two species *L. latidens* BIEDERMANN, from the Middle Miocene of such localities as Georgensmund and Engelswies, and *L. Lockharti* POMEL from the Lower Miocene (Burdigalian).

Besides the typical European Middle Miocene localities of Simorre, La Grive-St.-Albain, etc., lophodont species of *Listriodon* are known from Asia Minor² and from India³. PILGRIM⁴ has furthermore recently described two small bunodont species from India, and claims for one of them (*L. affinis* of the Bugti zone) a Lower Miocene or Upper Oligocene age, for the other (*L. Guptai* of the Kamliial zone) a Middle Miocene age.

In a single locality in the Ping Fan district of Kansu, there have now been found the remains of a gigantic pig which seems clearly to have been another species of bunodont *Listriodon*. There is no stratigraphical evidence as to the age of the beds from which it was collected. The material is for the most part in rather poor condition, but there is one very fine maxillary fragment (see text-fig. 1) and some isolated teeth in a good state of preservation. Several individuals are represented, of varying size.

That these remains are those of a *Listriodon* is at once made clear by the following characteristics:

- a) the shape of the very broad first incisors of both upper and lower jaws.
- b) the finely wrinkled enamel on the upper canines and the great breadth of the ventral enamel band.

¹ H. G. STEHLIN, "Geschichte des Suiden-Gebisses", Abhandlungen der Schweizerischen Paläontologischen Gesellschaft, vol. 26, 1898 p. 83 ff.

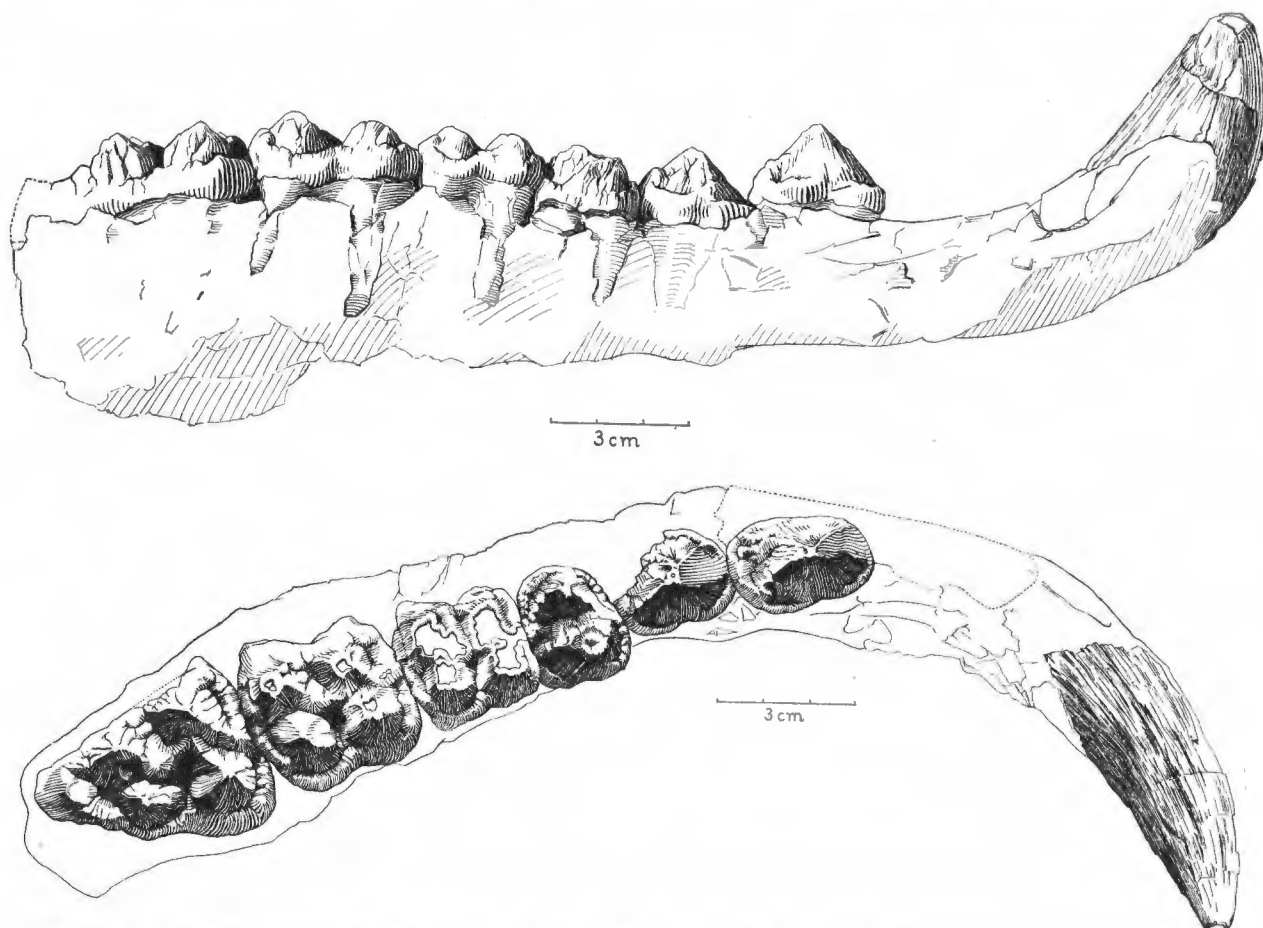
² From Tschanak-Kalesi, on the Hellespont; (see STEHLIN, loc. cit. p. 86 "teste CALVERT-NEUMAYR").

³ G. E. PILGRIM, "The Fossil Suidæ of India". Palæontologia Indica, New Series, Vol. VIII, 1926, pp. 31-34, where references to FALCONER'S and LYDEKKER'S previous descriptions are given.

⁴ G. E. PILGRIM, Loc. cit. pp. 34-36.

c) the shape of p^2 and p^3 , with their obliquely (instead of antero-posteriorly) disposed crests, and their very broad talons.

On the other hand there are certain conspicuous differences between this Chi-



Text-fig. 1. *Listriodon gigas*. Portion of left maxilla with canine and cheek teeth. The crown views of p^2 and m^3 restored from teeth of opposite jaw.

nese species and those hitherto known. Among these differences may be especially mentioned:

a) the absence of a definite cusp on the postero-internal border of the talons of p^2 and p^3 : the talons are very shallow basins with no marked wall on their lingual side.

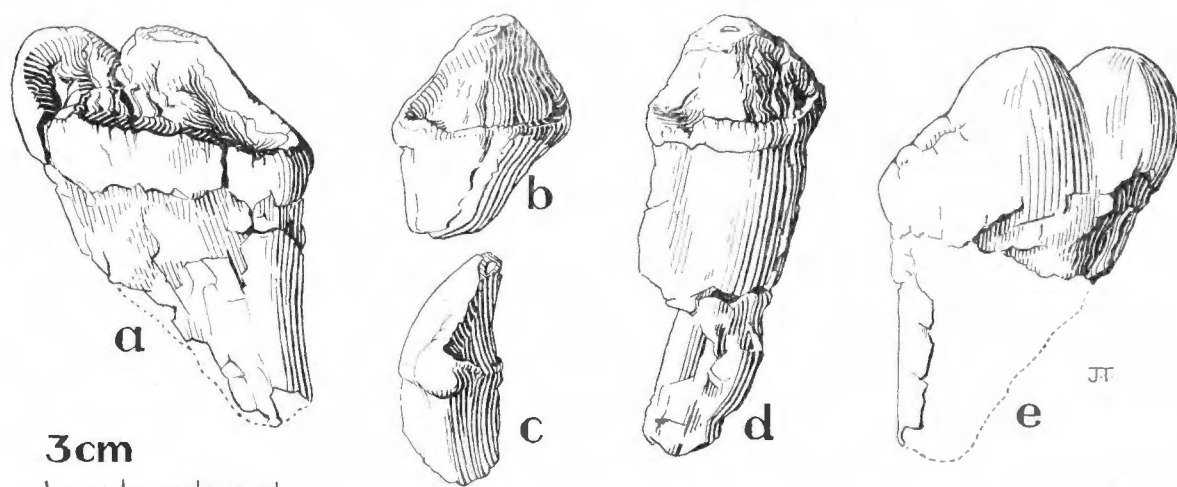
b) the possession by m^3 of a well developed talon.

c) the gigantic size: the head alone must have measured nearly two feet (over half a meter) in length.

There can thus be no doubt that we are dealing with a very distinct new species, for which I propose the name *Listriodon gigas*. From what we know of the evolution of other lines of Old World Suidæ, it is probable that the special characters just

listed are an advance on the conditions in the known European and Indian species of *Listriodon*. At the same time certain primitive characters have been retained: a first premolar is present in the mandible and the lower third premolar has no second cusp (deuteroconid) internal to the main cusp.

Whereas there seems to be a general agreement between the European and Indian species, both lophodont and bunodont, this giant species from Kansu appears to have evolved along rather different lines from any of them, and throws very little light on the phylogeny of the genus as a whole. It was probably derived from some Early Tertiary Asiatic form similar to the more primitive of the European bunodont species.



Text-fig. 2. *Listriodon gigas*. Upper incisor teeth, perhaps belonging to same individual as teeth in text-fig. 1. Natural size. a) and e) Lingual and labial views of left i^1 . d) Labial view of right i^2 . b) and c) Lingual and posterior views of right i^2 .

Thus we may expect it to be of later date than these latter, that is to say later than the Lower Miocene (Burdigalian). On the other hand, since no trace of it has been found in the typical Chinese *Hipparion* fauna localities, it is probable that the Ping Fan beds were earlier than the Pontian, though the difference might be a question of facies. It should be noted that a single first upper incisor of a *Listriodon* has been found in association with *Hipparion* in the Eichkogel deposits of the Vienna basin.¹

The material of *Listriodon* in the *Lagrelius* collection is as follows:

1. Upper Jaw.

a) Portion of left maxilla with the canine and cheek teeth (text-fig. 1): five upper cheek teeth (p^2 , p^4 , m^1 , m^2 and m^3) which appear to be those of the opposite maxilla

¹ M. VACEK. "Ueber Säugetierreste der Pikermifauna vom Eichkogel bei Mödling". Jahrb. d. k. k. Reichsanstalt, 1900, 50 Bd, 1 Heft, p. 182 and plate VII, fig. 3. STEHLIN (loc. cit. p. 483) has pointed out that the tooth tentatively ascribed by VACEK to *Helladotherium* is really the i^1 of a *Listriodon*.

of the same individual; a left i^1 and a right i^2 and i^3 which may also have belonged to the same individual (text-fig. 2).

These teeth are not much worn, and except for one or two breaks are in a good state of preservation. Both the second premolars are slightly broken, but that of the left side in a different way from that of the right side, so that a reconstruction has been possible in text-fig. 1. The same is true of the two third molars. The talon of the third left premolar is almost entirely broken away and there is no third right premolar, so that here no reconstruction has been possible; the little that is left, however, suggests that the talon was shaped as in p^2 , and this is the more probable as in other respects these two teeth are almost identical.

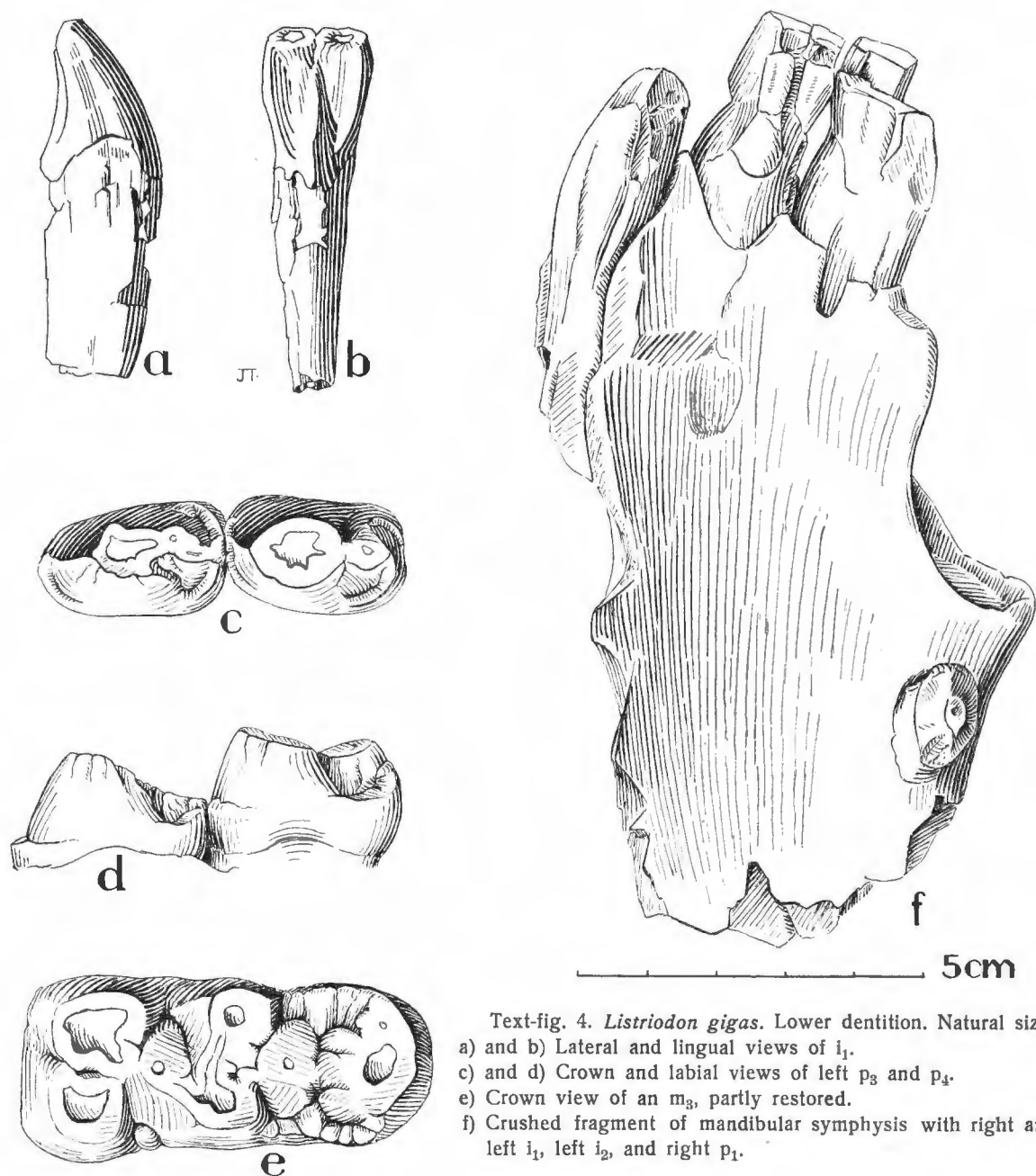
The alveolar border between the canine and p^2 has been broken and replaced by plaster, so that it is not possible to determine whether a p^1 were present or not.

i^2 and i^3 are very like one another in shape, though i^2 is rather stouter. They have the same strongly convex labial surface as i^1 and a similar, but narrower, internal cingulum; they are not such long teeth as i^1 however, and their biting edge is not divided into two cusps. They are very similar to the anterior lower premolars.

b) Part of another left maxilla with p^3 to m^3 . This belonged to a larger and older animal than the last, and is not in nearly such good condition. P^3 is again broken and is worn very low, but what is left bears out the view that in *Listriodon* the talon of this tooth carries no postero-internal cusp.



Text-fig. 3. *Listriodon gigas*. Distal end of right lower canine. a) labial, b) posterior, and c) lingual views. Natural size.



Text-fig. 4. *Listriodon gigas*. Lower dentition. Natural size.
 a) and b) Lateral and lingual views of i_1 .
 c) and d) Crown and labial views of left p_3 and p_4 .
 e) Crown view of an m_3 , partly restored.
 f) Crushed fragment of mandibular symphysis with right and left i_1 , left i_2 , and right p_1 .

2. Lower Jaw.

- a) Two partly broken lower canines, apparently those of an adult male (text-fig. 3).
 b) The badly crushed symphyisial region of a mandible, with broken i_1 of either side, yet more broken left i_2 , broken alveolus of right i_2 and of right canine, and very small broken right p_1 (text-fig. 4 f.).

This specimen shows that a p_1 was present in *Listriodon gigas* but gives no

certain information concerning the presence of i_3 , as the alveolar border in front of the canine is badly broken; there is room for an i_3 , however, and it was very probably present.

c) An isolated i_1 , uncrushed and of a younger animal than the last, showing well the robust proportions typical of this tooth in *Listriodon* (text-fig. 4 a and b).

d) Part of right mandible with broken alveolus of p_1 and with p_2 to m_3 ; the teeth are in very poor condition, m_1 and m_3 badly broken, p_2 and p_3 crushed.

e) An isolated left p_3 and p_4 , belonging to an older individual than the last specimen but in much better condition (text-fig. 4 c and d).

f) Some mandibular fragments with molar teeth, all very worn, crushed and broken; and a very worn and broken p_3 and p_4 . The m_3 in text-fig. 3 e is drawn from one of these fragments.

3. *Skeletal fragments.*

Parts of the skeletons of at least two individuals were collected in the same locality as the teeth. For the most part these are in poor condition. The better among them are figured in text-fig. 5.

This material consists of the distal ends of three humeri, a right scaphoid, the distal end of a tibia, two proximal ends and one distal end of calcanea, several phalanges and an ungual phalanx.

In pattern these agree with the corresponding bones of *Sus*, so far as the poor condition of the material permits comparisons, but the proportions are much more massive; especially noticeable in this respect are the very broad ungual phalanx and the wide sustentacular facet of the calcaneum.

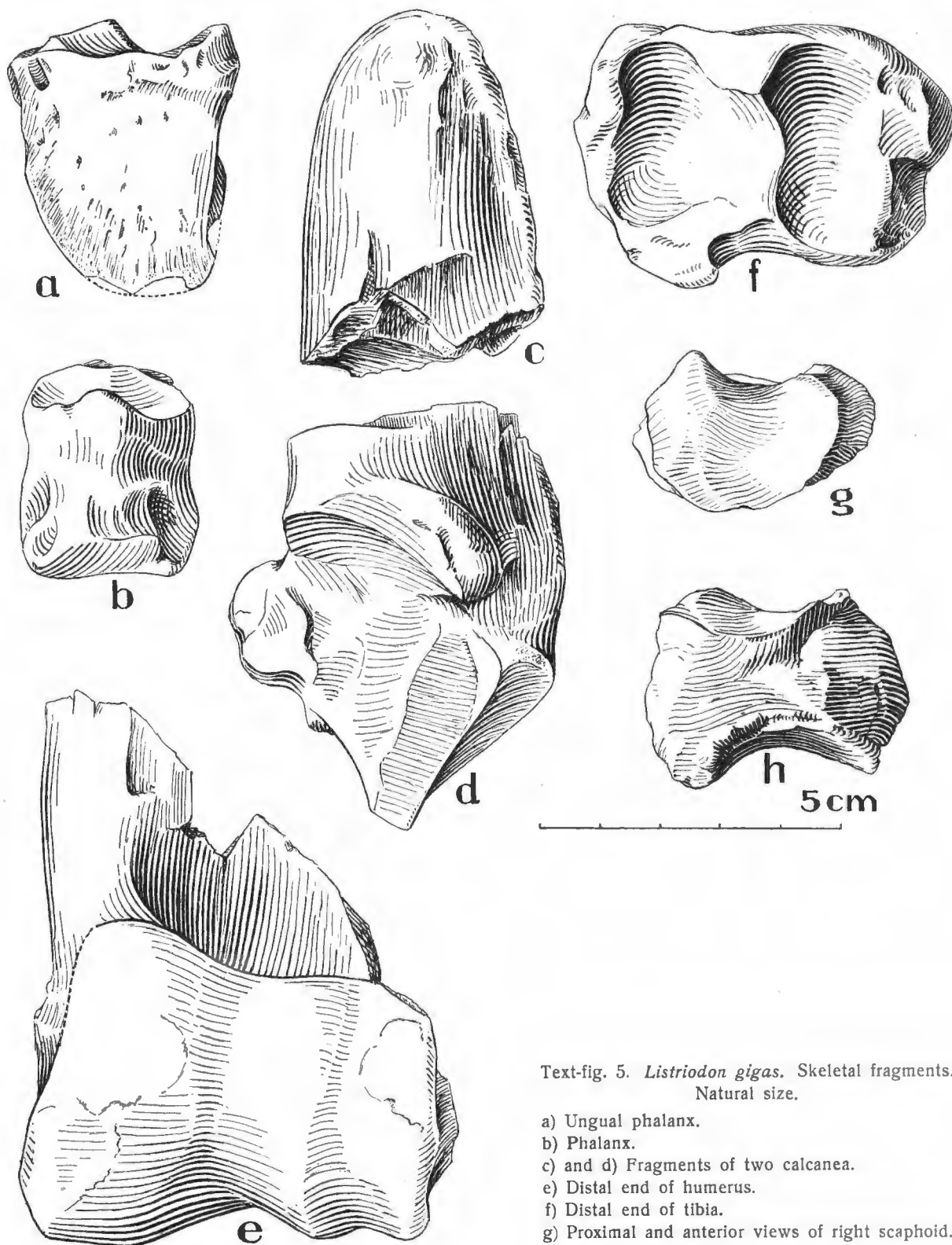
II. CHLEUASTOCHÆRUS STEHLINI gen. nov., sp. SCHLOSSER.

Localities.

- SHANSI. Pao-Te-Hsien. Locs. 30₂, 43₁, 44, 49, 109.
 „ Ching-Lo-Hsien. Loc. 48.
 „ Wu-Hsiang-Hsien. Locs. 71, 73, 78.
 HONAN. Hsin-An-Hsien. Locs. 11, 12, 13, 29, 35.
 KANSU. King-Yan-Hsien. Loc. 115.

This pig is of quite a unique type. Its skull, otherwise simple and primitive in structure, is at once marked off from that of any other known type of pig by the great bony arch over the canine teeth of the male and by the curious shelf-like expansion of the anterior end of the zygomatic arch.¹ Its feet were slender with very reduced lateral digits.

¹ Since this was written Dr. Pilgrim has told me that a somewhat similar expansion was present in the otherwise very dissimilar *Hippohyus*; (see his "Fossil Suidæ of India", plate XVI figs. 1, 2 and 3).



Text-fig. 5. *Listriodon gigas*. Skeletal fragments.
Natural size.

- a) Ungual phalanx.
- b) Phalanx.
- c) and d) Fragments of two calcanea.
- e) Distal end of humerus.
- f) Distal end of tibia.
- g) Proximal and anterior views of right scaphoid.

There seems to be every justification for placing this pig in a new genus, and this I have called *Chleuastochærus*,¹ in reference to the way in which the labial border of the maxilla and premaxilla are curved upwards over the canine teeth.

Among the teeth of Suidæ described by SCHLOSSER in his "Die fossilen Säugethiere Chinas" in 1903² were some belonging to a small form which he named *Sus Stehlini*. The isolated teeth which he figured are similar in size and proportions to those in the *Lagrelus* collection, and as the *Hipparion* fauna has yielded no other pig of appropriate proportions, it is probable that they did belong to the *Chleuastochærus* type. SCHLOSSER's *Sus microdon* appears to be merely a small variety of the same genus. It must be remembered however, that the age and locality of SCHLOSSER's material is uncertain, and also that very similar Suid teeth may belong to very different types of skull.

A. The Skull of *Chleuastochærus*.

A first idea of the size of the skull may be given by comparing it with that of *Babirussa*. One of the larger skulls, (for they vary considerably in size), is almost exactly the same length from *foramen magnum* to the canine teeth as a skull of *Babirussa* which I have by me for comparison, but it is not so broad across the zygomatic arches and the tip of the snout is not so elongated.

With the variations I shall deal later. The present description is based chiefly on the skull just mentioned, a beautifully preserved specimen from locality 49 in Pao-Te-Hsien, but with its snout broken off behind the canines, (see text-figs. 6, 7 and 8); the description of the canine and pre-canine region is therefore based on other material, which is also used in making the reconstructions given in text-figs. 16, 17 and 18.

Of Asiatic Oligocene and early Miocene pigs practically nothing is yet known, and while the teeth of European Oligocene and Miocene forms are fairly common, their skulls are known only very imperfectly. From the little we do know of these early European genera, however, and from the good skull material of the North American Upper Oligocene *Perchærus* (a primitive peccary, but still very close to the true Suine stock), it is evident that *Chleuastochærus* has retained many very primitive features.

Strikingly primitive, for instance, are the short snout, the flat contour of the top

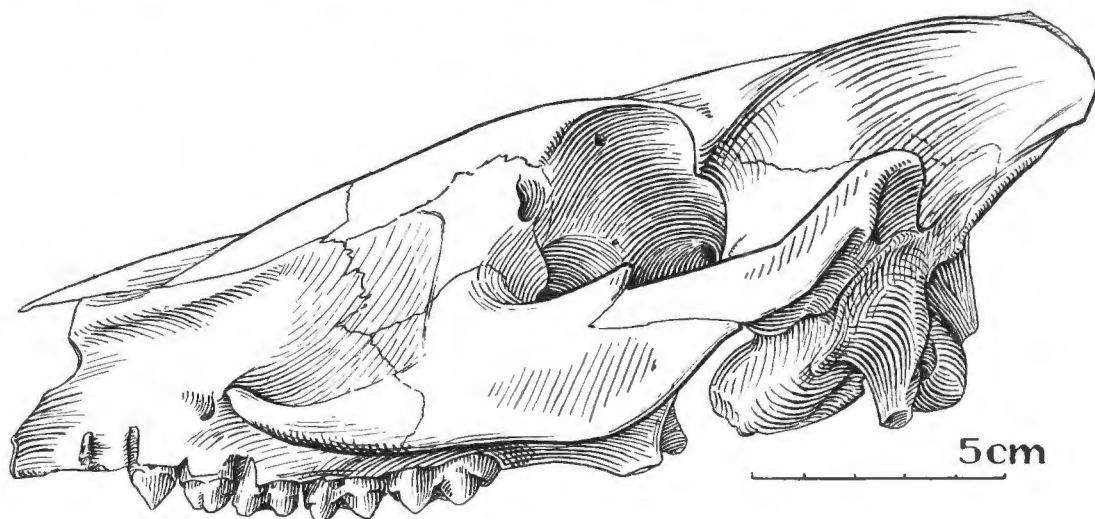
¹ Gr. *κλευαζω*, to mock by making wry mouths.

² M. SCHLOSSER, "Die fossilen Säugethiere Chinas nebst einer Odontographie der recenten Antilopen". Abh. k. bayer. Akad. Wiss. Math. Phys. Kl. Bd. XXII. p. 89.

of the skull, the low orbit, the short paroccipital processes, the forwardly rather than downwardly directed tympanic bullæ, and the slender lower jaw.

Premaxillæ and nasals. Examining the skull more carefully, it becomes clear that the shortness of the snout is largely due to the shortness of the premaxillæ, in which the three upper incisors are set close together. The hinder ends of the posterior palatine foramina are only a finger's breadth in front of the canine socket. The nasal bones are not only correspondingly short, but do not even reach forwards to the level of the tips of the premaxillæ as they do in modern Suidæ.

Brain case. No wild species of pig has the top of its skull bent upwards at the back so much as it is in the domestic varieties, but all have a tendency in that direc-



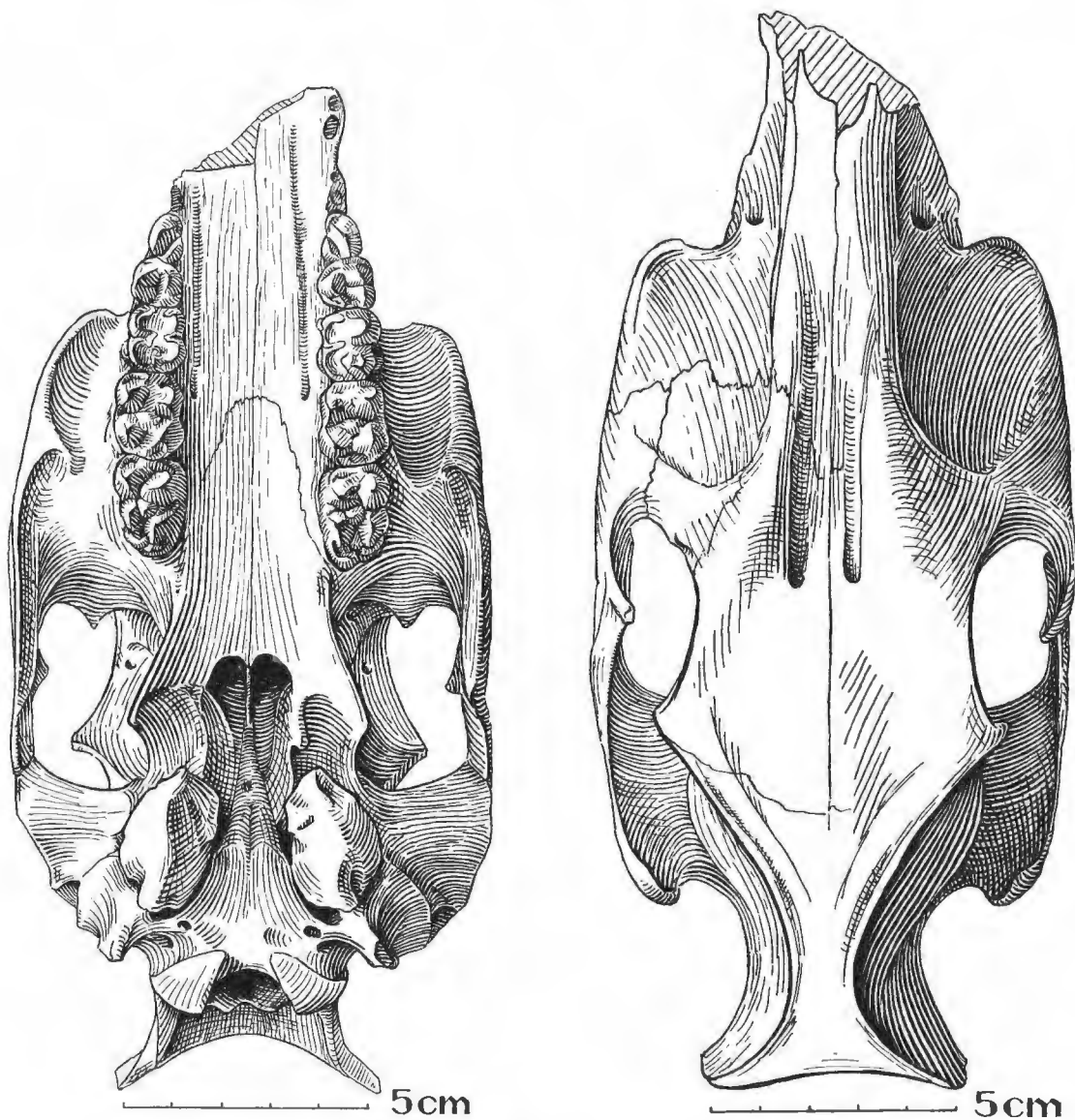
Text-fig. 6. *Chleuastochærus Stehlini*. Lateral view of the best preserved skull from loc. 49 in N. W. Shansi. Two thirds natural size.

tion. In *Chleuastochærus* the dorsal contour of the skull is an almost straight line. This would appear to be partly because the cerebral hemispheres are less expanded than in recent forms, but mainly because there is much less development of frontal, parietal and occipital air sinuses. When the skull is compared with that of modern Suidæ, it will be seen that the brain case is short and the orbits lie rather far back in relation to the face and palate.

Temporal region. As pointed out by MATTHEW¹ in his memoir on the Bridger Carnivora, an increase in size of the mammalian brain case, out of proportion to that in the size of the skull as a whole, calls for many other changes in the latter. The

¹ W. D. MATTHEW. "The Carnivora and Insectivora of the Bridger Basin, Middle Eocene". Memoirs of the Am. Mus. Nat. Hist. IX. 1909, p. 312.

orbit is pushed forwards not only because the brain is encroaching upon it from behind, but also because room must be left for the jaw muscles in the temporal fossa under the new conditions. In the Suidæ the orbit has moved forwards only very



Text-fig. 7 and 8. *Chleuastochærus Stehlini*. Ventral and dorsal views of the same skull as in text-fig. 6. Two thirds natural size.

slightly compared with that in many mammalian families, but enlargement of the temporal fossa has been brought about by the gradual shifting backwards of the glenoid surface on the skull, with the compression of the parts behind it, while the zygoma has become bowed outwards laterally. In these respects *Chleuastochærus* has again

retained a rather primitive condition, the glenoid surface lying comparatively far forwards and the parts behind it being but little compressed.

Less primitive in *Chleuastochærus*, or at any rate less like the known Oligocene Suidæ, and yet in striking contrast to the modern types, is the way in which the occipital crest projects far back over that part of the occipital surface immediately above the foramen magnum. This, together with the low parietal region and the forward position of the glenoid, indicates that the temporal muscle had a much more backward pull than in modern Suidæ. The temporal fossa is separated from the orbit by a very definite ridge curling downwards from the postorbital process of the frontal. This ridge is continuous below with the edge of the external pterygoid lamina of the alisphenoid, and meets this close to the anterior edge of the glenoid surface. In *Sus* and in *Babirussa* the more posteriorly placed glenoid surface is some way behind the root of the external pterygoid lamina: this allows the more dorso-ventrally directed temporal muscle to pass downwards in front of the glenoid to a firm embrace of the coronoid process of the lower jaw, and at the same time allows more room for the pterygoid muscles.

Pterygoid region. Since the mandibular articulation is far forwards, the external pterygoid muscles must have been short, and directed laterally rather than backwards. The absence of a powerful muscle area on the sphenoid process of the palatine, anterior to the pterygoid fossa, indicates that the origin of the internal pterygoid muscle was confined to that fossa and did not extend forwards in front of it as in modern Suidæ. Nor would a powerful internal pterygoid muscle be expected in view of the shallowness of the lower jaw.

Zygoma. As regards the masseter muscle, there are indications that it was the anterior, forwardly pulling part which was most strongly developed. The groove marking the area of origin of this muscle on the ventral surface of the zygoma extends forwards on the maxilla nearly to the hinder roots of the second upper molar. The posterior part of the masseter seems, on the other hand, to have been poorly developed. In modern Suidæ these posterior fibres take origin from the hinder end of the zygomatic arch lateral to the glenoid, and pass forwards and downwards onto the mandible, their direction of pull being almost at a right angle to that of the anterior fibres. In *Chleuastochærus* the posterior end of the zygoma is very narrow, since the jugal, from the hinder end of which these fibres would have arisen, tapers to a point beneath the squamosal at the anterior edge of the glenoid surface, instead of passing back lateral to that surface.

Thus while the pull of the temporal muscle was more backward in direction in

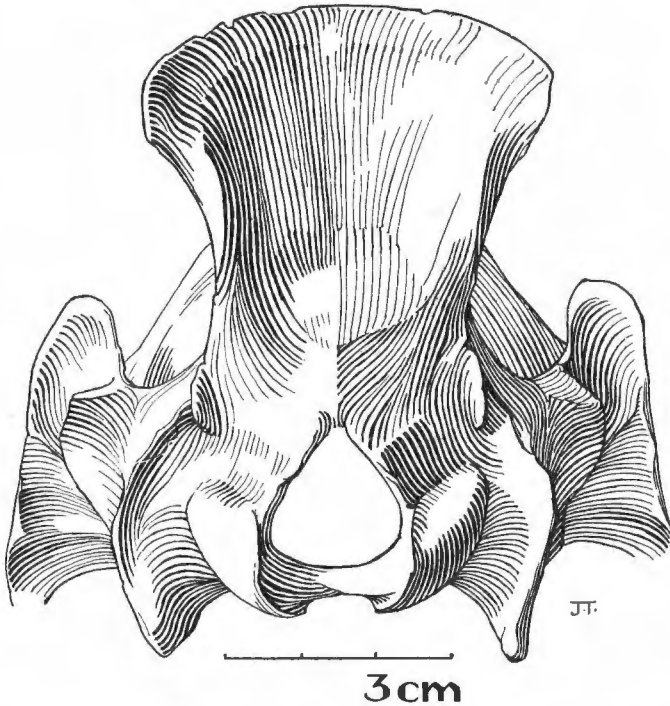
Chleuastochærus than in modern genera, the pull of the masseter muscle would seem to have been more forward.

Paroccipital process. The remaining masticatory muscle, the digastric, takes origin in *Sus* from the very tip of the slender, elongated paroccipital process, rather isolated from the neck muscles, which insert nearer the base of the latter. Its insertion is on the inner surface of the mandible, near the ventral border and beneath the third, or second and third lower molars, and its pull must be almost directly backwards parallel to the surfaces of the grinding teeth. In *Chleuastochærus* the paroccipital process is a comparatively short stump, as in Oligocene Suidæ, (though directed downwards as in all Suinæ, not backwards as in Dicotylinæ). This shortness is again probably correlated with the shallowness of the lower jaw and with the high level of the palate: in *Phacochærus*, the wart hog, where the lowering of the palate has reached an extreme, the paroccipital processes are also extremely long. The insertion of the digastric and its length and direction of pull seem to have been much the same as in *Sus*.

Meaning of these differences. The changes which have taken place in the various jaw muscles during the evolution of the Suidæ are probably in the nature of improvements in the crushing mechanism of which muscles, jaws and dentition play a part. The more vertically directed temporal and masseter muscles of *Sus* must increase the force with which the grinding teeth of the now much heavier lower jaw can be pressed against the upper grinding teeth. In *Chleuastochærus* these muscles, less vertically placed, would have aided in backward and forward mandibular movements, movements which are indicated by the wear on the incisor teeth to have been similar, to those in all recent old world Suidæ. In the latter these movements are probably effected not so much by the masseter and temporal as by the digastric and pterygoids, these last, as already noted, being more backwardly directed and more powerful muscles than they appear to have been in *Chleuastochærus*.

Tympanic region. It has already been said that the forward rather than downward direction of the long axis of the tympanic bulla is a primitive feature in *Chleuastochærus*. The most primitive Suid bulla that we know is that of the Oligocene Dicotylinae genus *Perchærus*, where it is a small smooth structure elliptical in outline. That of the contemporary Oligocene Suinæ — the European genus *Palæochærus* — had already been enlarged by the addition of a mass of cancellous bone to its ventral surface, and was pointed anteriorly, and grooved as in recent Suidæ where the stylohyoid cartilage was pressed against it. The bulla of *Chleuastochærus* has had yet more cancellous bone added to its ventral surface, and a comparison with modern forms shows that the change in direction of the long axis of the bulla is chiefly due to the

continued addition of this cancellous tissue. Such downward rotation of the bulla as has actually taken place is perhaps in response to the lowering of the palate and consequent change in direction of the *tensor veli palati* muscle. This muscle takes origin immediately in front of the bulla between the foramen ovale and the groove



Text-fig. 9. *Chleuastochærus Stehlini*. Occipital view of the same skull as in text-figs. 6 to 8. Natural size.

for the Eustachian tube; it passes forwards and downwards in the pterygoid fossa, close against the antero-dorsal surface of the bulla and medial to the internal pterygoid muscle, reaching the soft palate by a tendon which curves around the ventral edge of the hamular process. The palate being at a lower level the muscle would have to take a more ventral direction, and to make room for it the bulla also would have to be more ventrally directed.

Occipital surface. The remains of another Oligocene character in *Chleuastochærus* is the small knob on either side of the occipital surface, about a finger's breadth above the occipital condyle. Each knob marks the ventral termination of the lateral occipital crest,

which is not, as in modern *Suidæ*, smoothly continuous with the sharp edged, ear like projection of the squamosal at the back of the zygoma over the external auditory meatus.

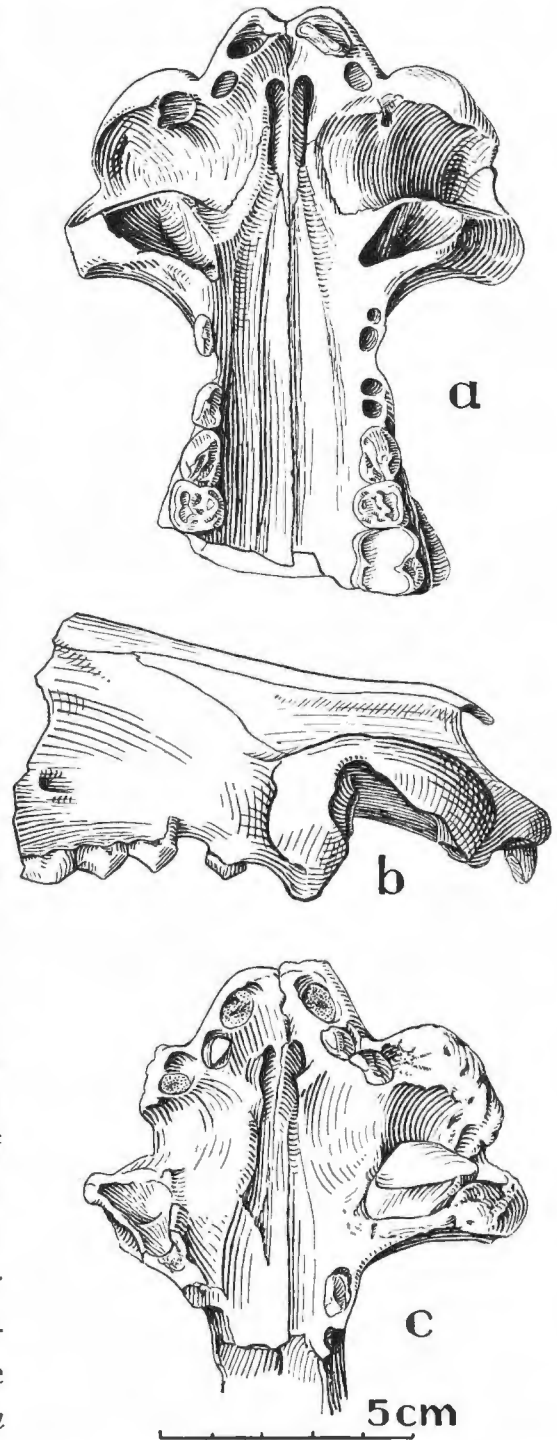
In the Aquitanian *Palæochærus* the lateral occipital crests end in freely projecting knobs just above the occipital condyles, while the dorsal edge of the zygomatic process of the squamosal arises quite independently from the wall of the brain case some way in front of these crests.¹ *Chleuastochærus* is intermediate between *Palæochærus* and recent *Suidæ* in this respect, for although each lateral occipital crest still terminates freely above the condyles, the dorsal edge of the zygoma arises from the brain case so close to the crest as to be almost continuous with it at about half its height. If it were to arise yet a couple of millimeters further back, so that the continuity were

¹ See H. S. PEARSON, "On the skulls of Early Tertiary *Suidæ* — ——" *Phil. Trans. Roy. Soc. Lond., ser. B.*, vol. 215. 1927, text-fig. 6.

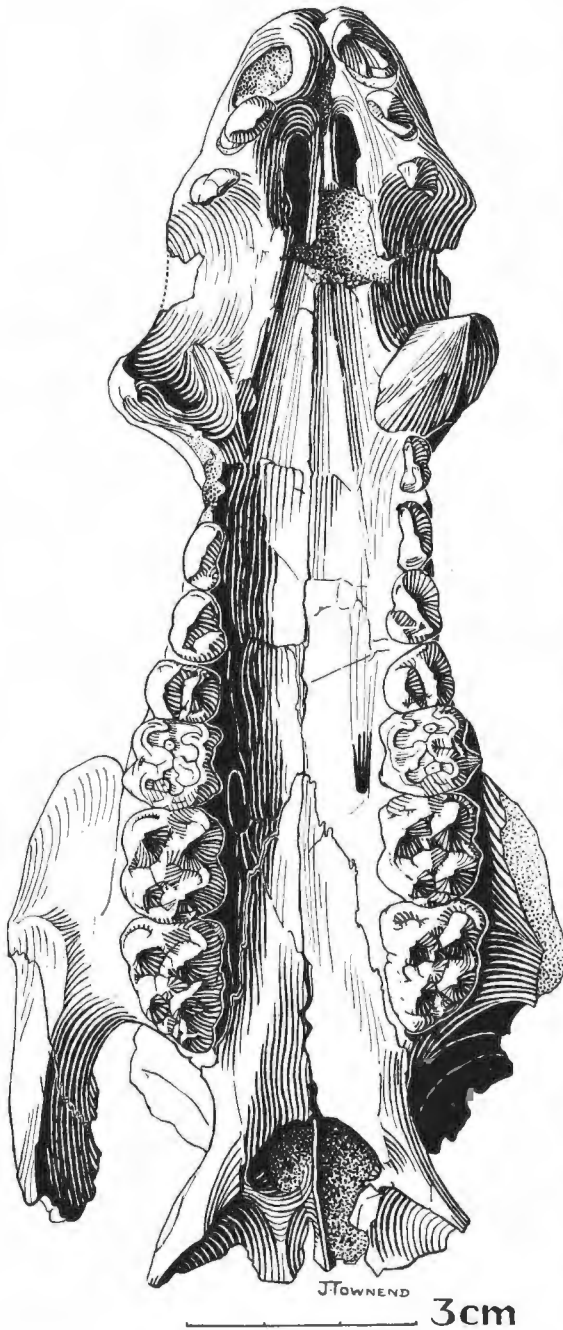
complete, and if the ventral, freely projecting end of the lateral occipital crest were to disappear entirely, conditions would be as in recent Suidæ.

This change in the appearance of the occiput would seem to be simply a part of the process, already referred to, of shifting backwards the glenoid articular surface, and compressing what lies behind it, in order to make more room for the temporal muscle. The united zygomatic and occipital crests would at the same time afford a stronger and more extensive attachment for both the temporal muscle and the neck muscles, the former pulling on it from in front, the latter from behind. The neck muscles become of increasing importance to a head which is not only employed in rooting in the ground, but also needs to be jerked forcefully sideways when its great projecting canine tusks are used as weapons. *Chleuastochærus* had no projecting tusks, and it is doubtful if it could have used its snout for rooting, but the occipital characters may have already established themselves in the Suid stock before this peculiar genus branched off from it.

The peculiar snout and canine teeth. In modern Suidæ we are accustomed to a crest of maxilla above the root of the superior canine. In *Potamochoærus* this is raised into a high wall. In *Babirussa* it forms a socket to the peculiar upturned canine. Some of the skulls of *Chleuastochærus* have quite a unique arrangement. The upper canines resemble those of *Hyotherium simorreense*: they are very short stumps, directed outwards from the palate at an angle of about 45 degrees, but not curved; their worn surface faces straight forwards. All the upper



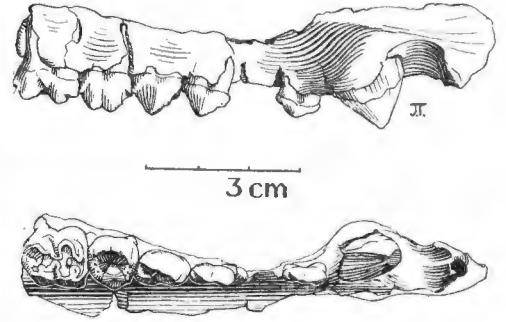
Text-fig. 10. *Chleuastochærus Stehlini*. a) and b) Ventral and lateral views of a male snout from loc. 49 in N. W. Shansi. c) Ventral view of an older male snout from loc. 49 showing "cauliflower growth". Two thirds natural size.



Text-fig. 12. *Chleuastochærus Stehlini*. Female skull from loc. 43₁ in N. W. Shansi. Natural size.

canines that I have seen are truncated abruptly by this surface, which was evidently kept worn by continual contact with the much narrower trenchant lower canine. The roots are grooved in a manner similar to that in *Hyotherium*, but are considerably shorter than in that genus; their

very shallow sockets are sometimes divided at the bottom into two distinct hollows by a low ridge. These short canines are car-



Text-fig. 11. *Chleuastochærus Stehlini*. Ventral and lateral views of fragment of female snout from locality 49 in N. W. Shansi. (For comparison with text-fig. 10.) Two thirds natural size.

ried out laterally in front of the cheek teeth by the projecting alveolar border of the maxilla. But the maxilla does not only project as a socket to the tooth: in some of the skulls it forms part of a great arch or dome, completed in front by the premaxilla, and overhanging both the upper canine and the slender trenchant crown of the lower canine, the latter no longer than that of a modern peccary. The border of this arch is thickened and rough, a condition which may be much exaggerated by exostosis, so as to resemble the condition called by the human pathologist "cauliflower growth" (see text-fig. 10 c); the older the animal (as judged by the wear on its cheek teeth) the thicker and more prominent is this arch likely to be.

In those skulls which have the broad arch over the upper canine this tooth is also very broad and is circular in transverse section. In other skulls, presumably those of females, the upper canines are only about half this breadth, the section being

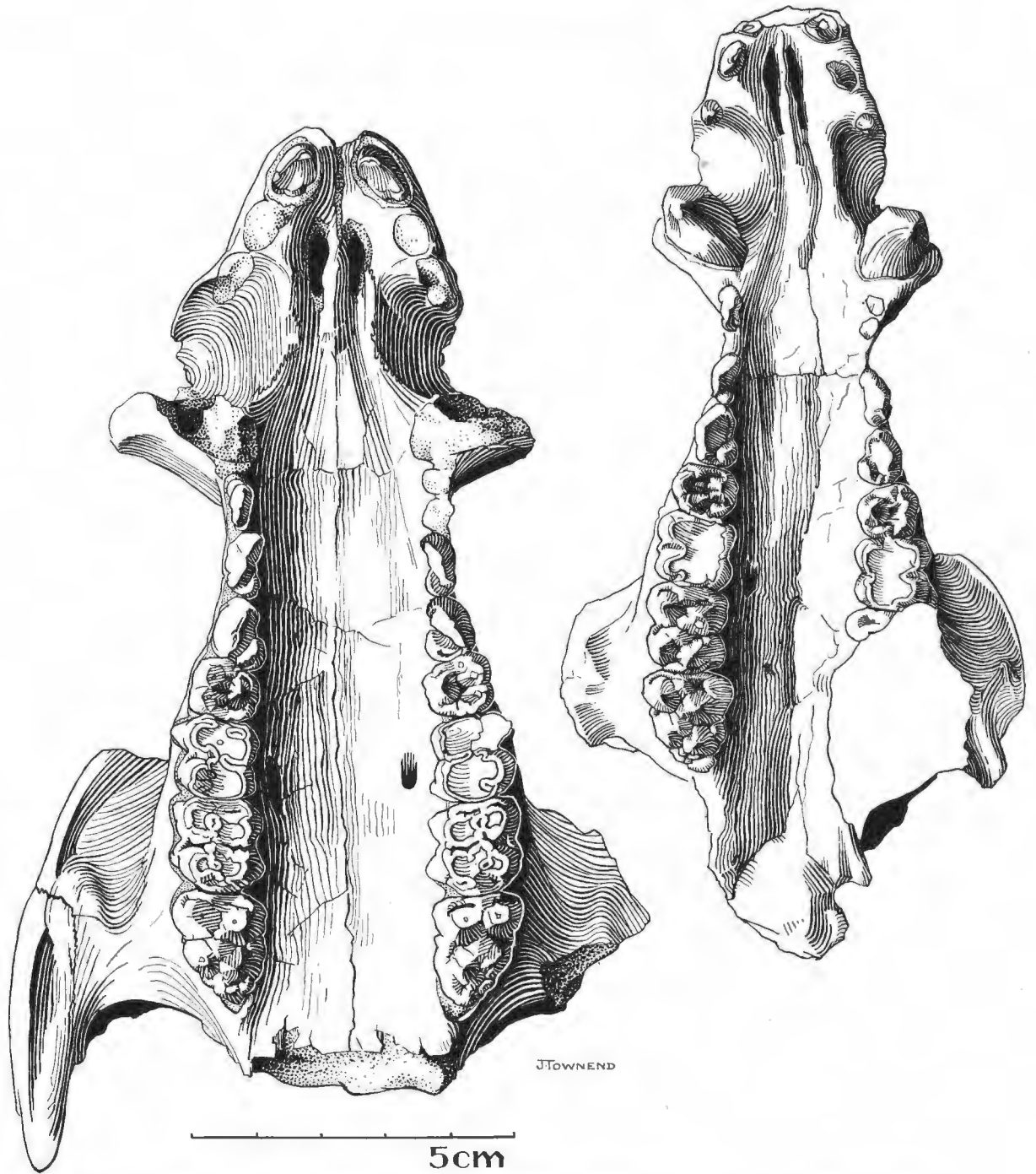
elliptical, while the arch above them is correspondingly unimportant and may be little more than a shallow depression in front of the upper canine for reception of the lower (text-fig. 11). A condition very similar to this latter is found in some species of the Oligocene Dicotyline *Perchærus* and is still retained in recent peccaries. In the Suine stock the first stage in the evolution of such an arch — a small niche in front of the upper canine — is beautifully shown in the skull of a small species of *Palæochærus* from the Aquitanian of St. Gérard-le-Puy, now in the British Museum (where it is labelled *Hyotherium typum* No. 34961 a). In the skull of the Miocene *Hyotherium simorreense* figured by FRAAS¹ (from Steinheim, in the Stuttgart Naturhistorisches Museum) the niche has become a wide recess over which the slightly thickened border of the maxilla projects a little, but not nearly so much as in any of the skulls of *Chleuastochærus*.

Those skulls of *Chleuastochærus* which show the maximum development of the supra-canine arch all come from locality 49 in the neighbourhood of Pao-Te-Hsien in N. W. Shansi. In other skulls coming from this same locality, or from other localities in the same neighbourhood (text-fig. 12), both arch and upper canine are very feebly developed, and it seems clear that in this case the difference must be one of sex, though individual variation is also considerable. From Honan and the more southern localities in Shansi, where the local races of these pigs appear to have been smaller (see section III below), no skulls have so far been collected in which the arch is nearly as well developed as in the male skulls from N. W. Shansi, though again it varies considerably from one individual to another (text-figs. 13 and 14). On the other hand, a single skull from Eastern Kansu (text-fig. 14 a) has a broad arch although it is that of a very small pig.

In the skulls where this arch attains its maximum development, neither the upper nor the lower canine can have projected as a tusk.

Before discussing this condition further, it will be as well to consider the other peculiar character of the *Chleuastochærus* snout, namely the broad shelf of maxilla anterior to the zygomatic arch. This shelf, which has a thickened edge, projects laterally from above the roots of the first two molar teeth and is continuous behind with the zygomatic process of the maxilla. In front it is abruptly rounded off just posterior to the infra-orbital foramen. The dorsal surface of the shelf slopes up gradually onto the side of the snout, where a shallow preorbital depression, not very different from

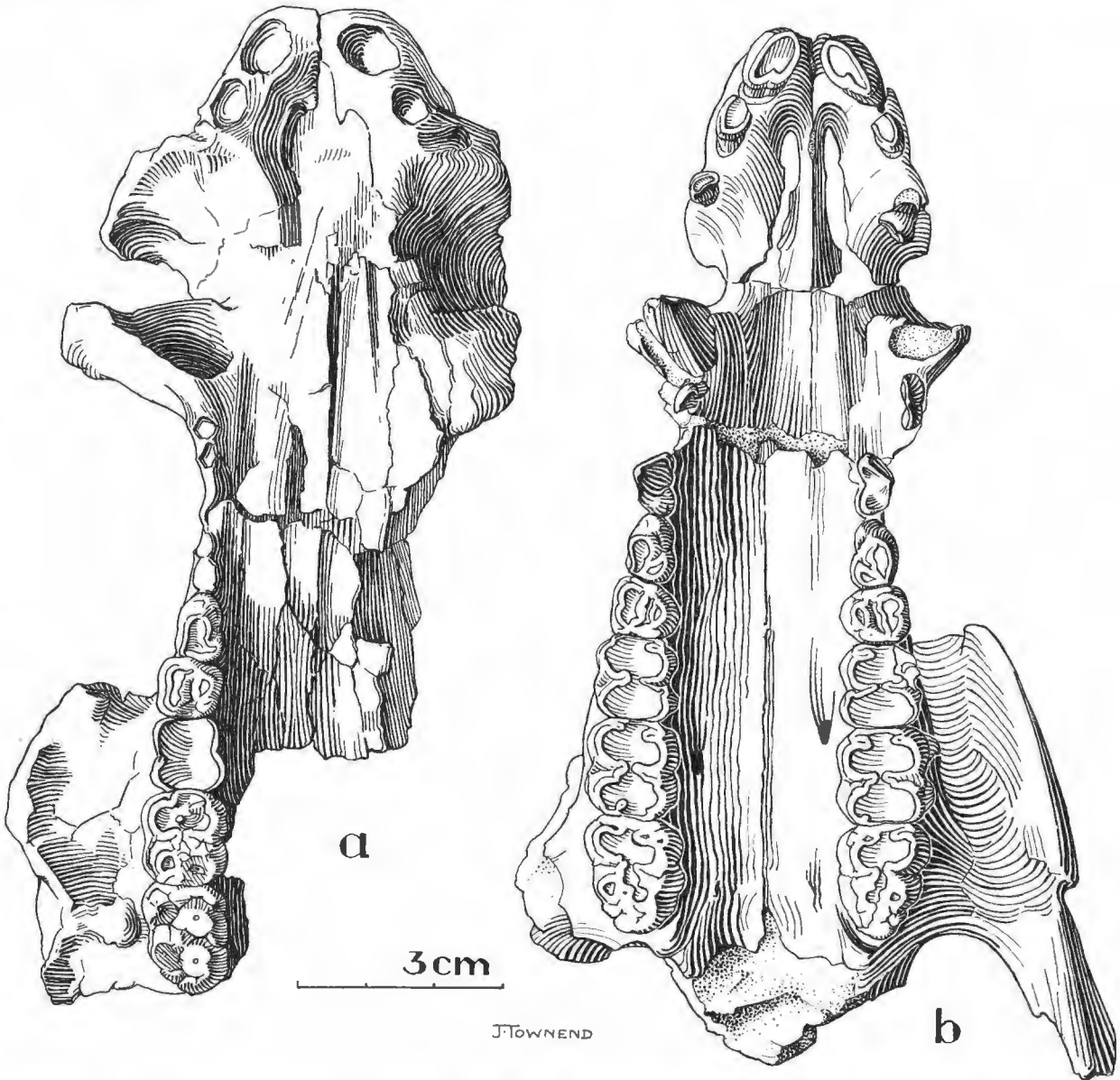
¹ O. FRAAS, "Beiträge zur Fauna von Steinheim". Jahreshefte des Ver. f. vaterl. Naturk. in Württemberg. Jahrg. 41. See also H. S. PEARSON, "On the skulls of Early Tertiary Suidæ — —" Phil. Trans. Roy. Soc. Lond., Ser., B. vol. 215, 1927, text-fig. 13.



Text-fig. 13. *Chleuastochærus Stehlini*. Male and female skulls from loc. 73 in S. E. Shansi. Natural size.

that in *Sus*, marks the position of the *levator labii superioris* (*levator rostri*) muscle. The hinder end of this depression includes about half the facial exposure of the lachrymal, which is a long one since the orbit is placed far back. It also includes the anterior extremity of the jugal, just as in *Sus*.

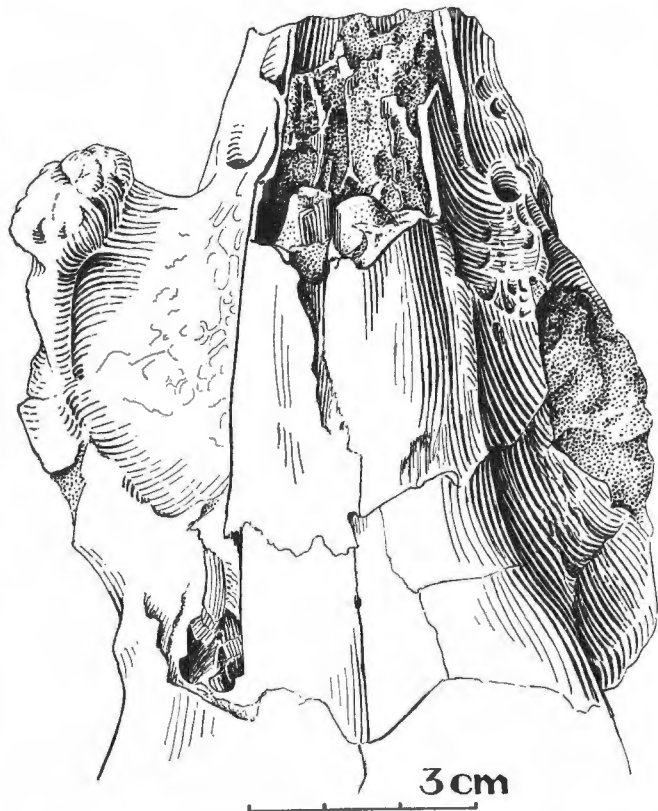
The broad maxillary shelf of *Chleuastochærus* seems to represent the comparatively slight ridge which in *Sus* forms the lower boundary of the preorbital depression and itself gives origin to the *dilatator naris lateralis* muscle. In *Sus* a third



Text-fig. 14. *Chleuastochærus Stehlini*. a) Male skull from loc. 115 in E. Kansu, and b) female skull from loc. 29 in N. Honan. Natural size.

snout muscle, the *depressor rostri*, takes origin just below the latter from a well-marked area immediately anterior to that for the masseter. It would seem, therefore, that the *depressor rostri* muscle of *Chleuastochærus* took origin from the ventral surface of the prezygomatic maxillary shelf. From here it must have passed forwards

and slightly upwards for its tendon to slide over the pulley-like surface of the great supra-canine arch and then to pass downwards again into the skin of the snout beneath the nostrils. Half way up the narial border of the premaxilla there is in some of the skulls a slight groove, which probably lodged this tendon, and which suggests that it was a strong one. In *Sus* the *depressor rostri* meets its fellow anteriorly



Text-fig. 15. *Chleuastochærus Stehlini*. Fragment of snout of old individual from loc. 49, showing "cauliflower growth" on prezygomatic shelf, and honeycomb marking on facial plate of maxilla. Natural size.

beneath the nostrils; the two together cause these to contract and at the same time they depress the disc-like tip of the mobile snout with its *os rostri*; the snout is elevated by the *levatores rostri*, whose tendons flatten out over the tip of the nasals and are attached to the anterior part of the *os rostri*. Lateral movements of the snout and dilation of the nostril are in *Sus* effected by the *dilatator naris lateralis*, the origin of which, as described above, is from the prezygomatic ridge, and which breaks up at the level of the canine into a fan of fine tendons passing out into the skin at the side of the snout.

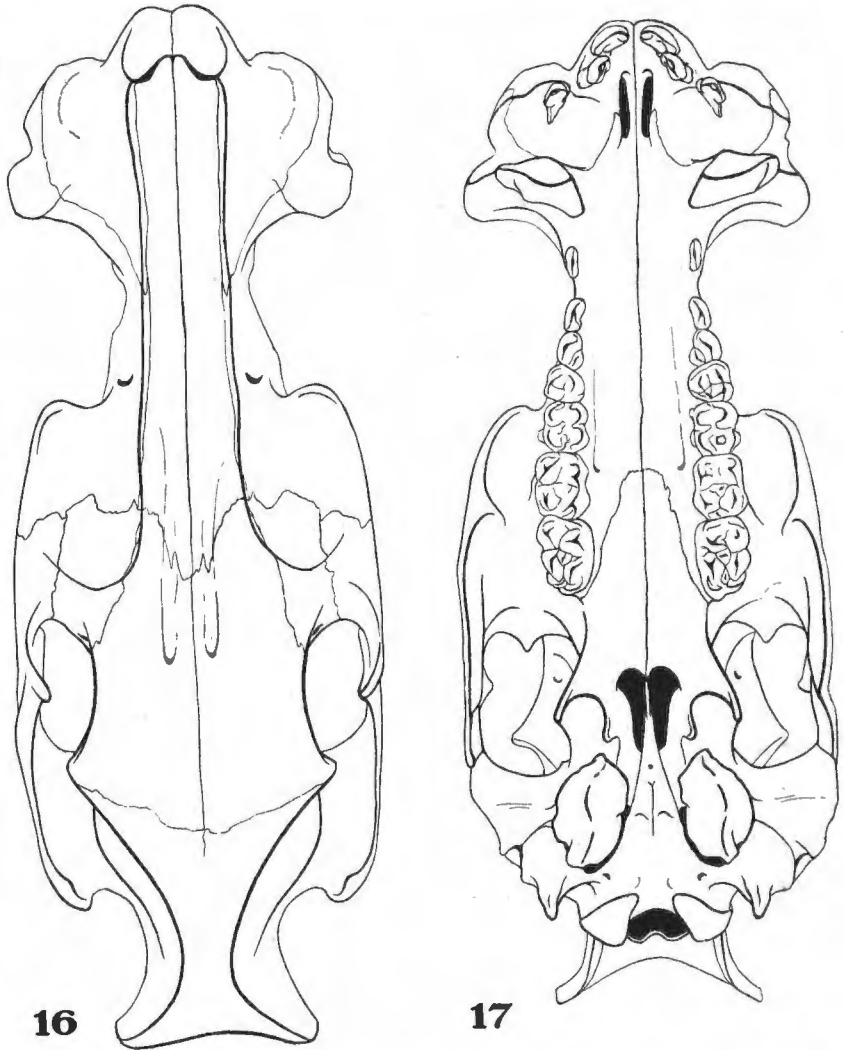
It is questionable whether the *dilatator naris lateralis* were present in *Chleuastochærus*, or at any rate were of such importance. The *levator* and *depressor rostri* were evidently both important muscles separated posteriorly by the broad prezygomatic shelf of maxilla. If this shelf

were not developed, — that is to say, if there were no more than a slight ridge here as in *Sus*, — the area for the origin of the *depressor rostri* muscle would be a very small one, since the alveolar portion of the maxilla is so much shallower than in *Sus*, where the palate lies at a lower level. It is possible therefore that the prezygomatic shelf of *Chleuastochærus* is correlated with the need for a powerful *depressor rostri* muscle. This seems a more probable explanation of the shelf than an attempt to associate it with a *dilatator naris lateralis* muscle. There is no indication that any such muscle arose on the edge of the shelf between the *depressor* and *levator rostri*, for the bone here has all the appearance of having been

directly subcutaneous, in some of the skulls rounded and smooth, in others roughened and covered with very fine pits. In one skull the thickening and roughness are so exaggerated by exostosis as to suggest a pathological condition (text-fig. 15); the very worn teeth of this skull show that it belonged to an old individual, and we have seen that a similar exostosis may characterise the border of the supra-canine arch in old male individuals. That the margin of the shelf is thickened at all would seem to be in order to give a stronger grip to the fibres of the *levator* and *depressor rostri* muscles arising above it and below it.

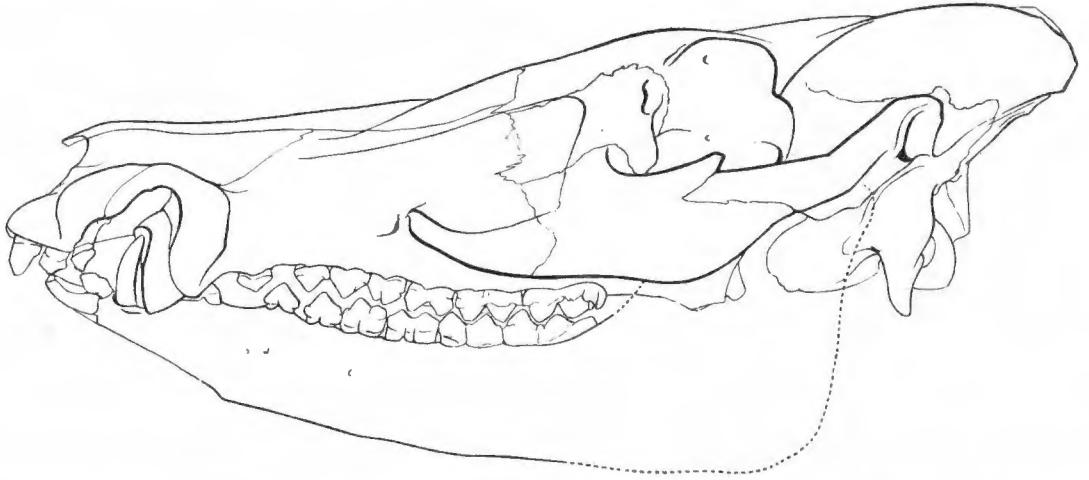
This brings us back to the problem of how *Chleuastochærus* used its peculiar snout. In spite of the well developed *levator* and *depressor rostri* muscles, it can hardly have been used as a digging organ like the long pointed snout of *Sus* with its fleshy terminal disc; at any rate it cannot have been such an effective one. The short premaxillæ are rounded off in

front of the extremely broad canine region, and the nasals end some little way posterior to the premaxillæ. In *Sus* the pointed tips of the nasal bones reach almost as far forwards as do the elongated premaxillæ, and between the tips of the nasals above and the premaxillæ below is wedged the little prenasal bone or *os rostri* which supports the fleshy disc. As to whether such a prenasal bone were present in *Chleuastochærus* one cannot be quite sure, but there is no trace of one attached to the end of any of the eleven snouts in the *Lagrelius* collection, and the general shape of this region makes it unlikely. It is still more un-



Text-figs. 16 and 17. *Chleuastochærus Stehlini*. Reconstruction of dorsal and ventral views of male skull from loc. 49. One half natural size.

likely that there can have been a fleshy terminal disc, and the absence of such a disc would perhaps account for the absence of a *dilatator naris lateralis* muscle. Probably the animal was provided with a mobile upper lip like that of a horse or ruminant. At the same time it is clear that the food, whatever it may have been, was of a harsh nature, for the teeth of old individuals are well worn, just as they are in recent species of *Sus*. In chewing this food the mandible was evidently capable of extensive lateral

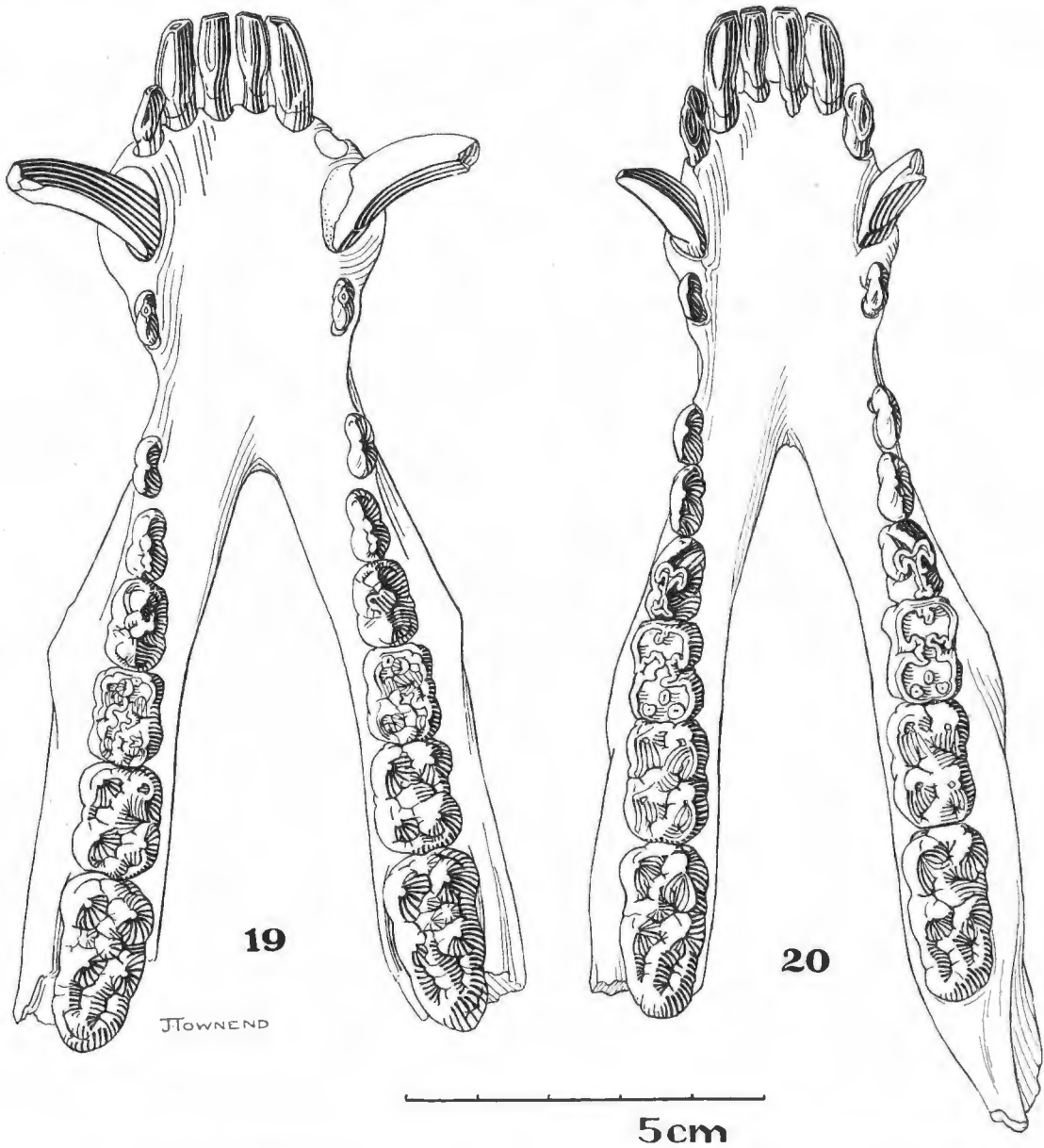


Text-fig. 18. *Chelustochærus Stehlini*. Reconstruction of lateral view of male skull from locality 49. One half natural size.

movement, for in all cases the upper canines, even the very broad ones in the male skulls from N. W. Shansi, have been worn flat right across their anterior face by the very much narrower lower canines. Backward and forward movements of the mandible are also indicated by the appearance of the incisor teeth, which, just like those in modern wild pigs, are worn not only flat across the tips but also on their backwardly slanting lingual surfaces: indeed, in some very old individuals the incisors are mere stumps, all but worn down to root level.

It thus probable that these animals were adapted to an omnivorous diet much like that of pigs today, but that they had not the rooting powers of modern pigs. The supra-canine arch can have had nothing to do with feeding habits, since it is characteristic only of the males. Indeed it is hard to find any functional explanation of this arch; fighting males might possibly have used it for butting one another, but this is not very likely, since the extreme slenderness of the snout immediately posterior to the arch makes the skull very weak here, as the frequent breakage at this point in the fossil skulls bear witness. Even if not directly used as a weapon, however, the projecting arch, which appears to have lain immediately under

the skin, was probably often subjected to hard knocks, and this may account for the fact that in some of the older individuals its rim is so much thickened and roughened



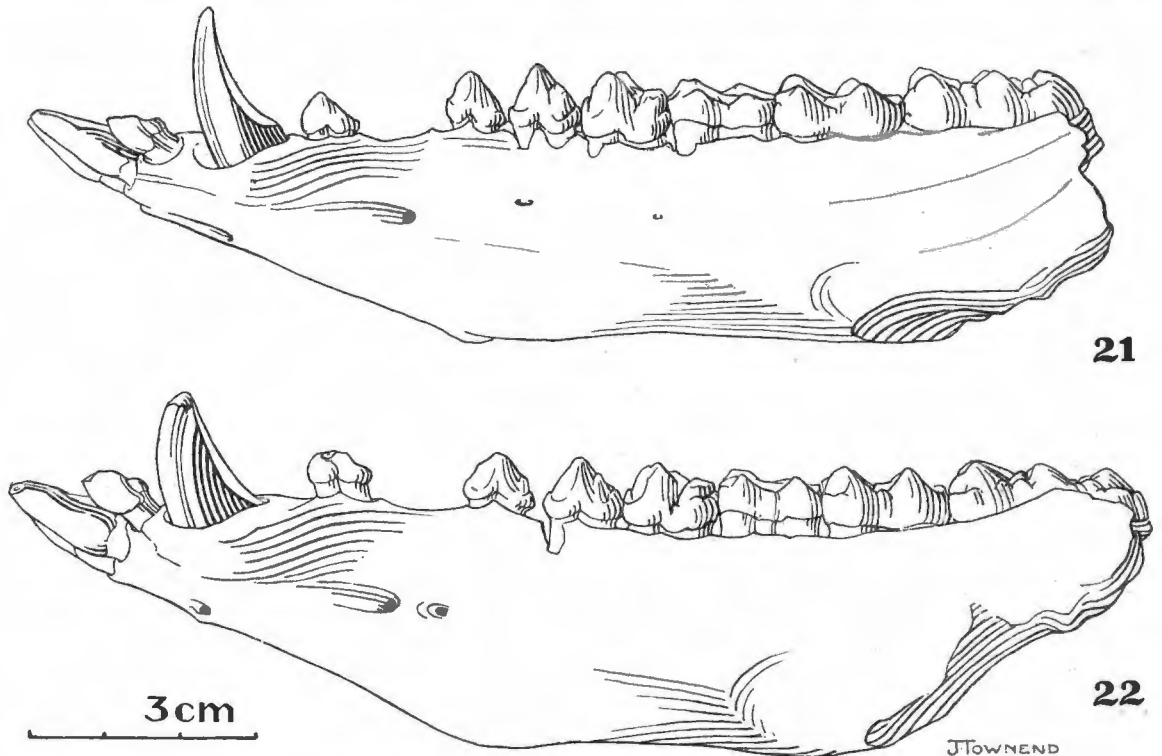
Text-figs. 19 and 20. *Chleuastochoærus Stehlini*. Crown views of male and female mandibles from loc. 49. Natural size.

with exostosis as to wear an almost pathological appearance, as if it had suffered from periosteal inflammation (text-fig. 10 c).

Mandible. The angular, coronoid, and condylar regions of the mandible are not retained intact in any specimen. Text-figs. 19 and 22 represents what appears to be the mandible of a male pig, text-figs. 20 and 21 that of a female, but it is not in

all cases so easy to distinguish the sexes. In the males the symphysis tends to be broader and the alveolar border to project more around the canines, but there are one or two jaws in which these characters show an intermediate degree of development and which therefore cannot be confidently assigned to either sex. Age differences of course also play a part.

Teeth. Except for the upper canines, there is nothing remarkable about the teeth



Text-figs. 21 and 22. *Chleuastochærus Stehlini*. Lateral views of female and male mandibles from loc. 49. Natural size.

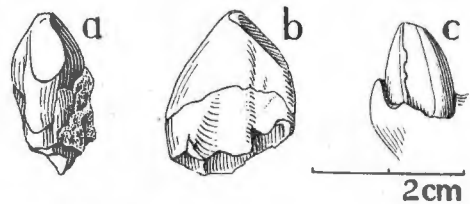
of *Chleuastochærus*. They are rather simple and primitive, easily derivable from those of some *Palæochærus*-like ancestor.

The three upper incisors are placed close together, an interval of not more than one or two millimeters between i^1 and i^2 , and of two or three millimeters between i^2 and i^3 . I^1 is the largest of the three, its shape very similar to that of an i^1 of *Sus* or *Dicotyles*, but its surfaces quite smooth and its edges sharp; in older skulls the back of the tooth is worn flat from the tip almost to the root. I^2 and i^3 are simple pegs, very similar to one another in shape, but i^3 a reduced and apparently almost functionless tooth lying lateral to i^2 and within the supra-canine arch, where a considerable length of its root is often exposed on the anterior, backwardly facing slope.

In the older skulls they are both worn flat across the tip, but i^2 is always much more worn than i^3 , which lies lateral to the lower incisors when the mandible is closed, so that in old skulls, owing to the lack of wear, it tends to project down below the level of the other upper incisors.

The lower incisors are procumbent and pressed very close to one another. The roots project a considerable distance out of the sockets. I^2 is both stouter and longer than either of the others, reaching forwards so that its tip is in a line with that of i_1 . I_1 and i_2 are worn transversely across the tips; i_2 also shows wear backwards from the tip along the upwardly directed lingual surface. I_3 is weaker than the others, peg-like, and little worn even in quite old jaws; it is usually less than half a centimeter in front of the canine.

The short stumpy nature of the upper canine in both sexes, and its much greater breadth in the male than in the female, have already been described, (p. 19). Text-figs. 11 and 23 show the disposition of the enamel in two female canines from locality 49, both apparently young animals; in none of the other canines preserved is it shown distinctly. The lower canines are of markedly "scrofic" type in those canines which clearly belong to males; those of the females have rounded outer angles and may be termed "verrucose", but canines of intermediate character also occur, in jaws which the wear on the molar teeth shows to be quite adult.



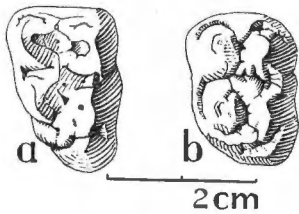
Text-fig. 23. *Chleuastochærus Stehlini*. a) and b) Anterior and lingual views of isolated upper right canine of female from loc. 49. c) Posterior view of upper right canine in maxilla of female from loc. 49. Natural size.

In the upper jaw the diastema between p^1 and the canine socket varies from 1 mm. to 8 mm.; the diastema between p_1 and p_2 varies from zero to 6.5 mm. The diastemata in the lower jaw are correspondingly variable. When the jaws were closed the small first lower premolar seems to have lain almost directly mesial to the upper canine.

The cheek teeth as a whole are characterised by few accessory cusps and folds: such as they have are very variable. Pl. I, figs. 2 and 3 will, I think, give a better idea of them than any description. It may be noted that the talons (postero-internal cingula) of the first three upper premolars, all two-rooted teeth, are developed to a very variable degree in different individuals; also that the paracone and metacone of p^4 ("protocone" and "tritocone" of Scott's nomenclature), though usually two well-defined cusps, are sometimes barely distinguishable from one another, the degree of separation being variable (see Pl. II, figs. 1 and 2, and text-fig. 13). P_4 shows the same sort of variation as p^4 ; usually the main cusp is distinctly cleft at the

tip, so that there appear to be two twin cusps, the inner one (deuteroconid) lying postero-lateral to the outer one. This cleft is not always equally clear-cut, however, and in at least one case (from locality 30 in the district Pao-Te-Hsien, see Pl. II, figs. 3 and 4) it is so slight a groove that the inner and outer cusps are to all intents and purposes confluent. When both are clearly separate the condition is similar to that which is typical for *Palæochærus* and for *Hyotherium Scæmmeringii*, and which has been regarded as primitive by Stehlin.

Variations in the size and proportions of the molar teeth are dealt with in section III below. Here it is sufficient to note that m^1 , as in all later Suidæ, retains most nearly its primitive squareness, whereas m^2 and m^3 have become each more elongated than the other. The talon of m^3 , as in all Suidæ recent and fossil that I have examined in quantity, shows a large amount of variation: it may be important and divided into a number of cusps, or little more than a posterior cingulum (see text-fig. 24). The talonid of m_3 though always a large and important part of the tooth, is equally variable. Striking differences may also be seen between third molars on opposite sides of the same individual.



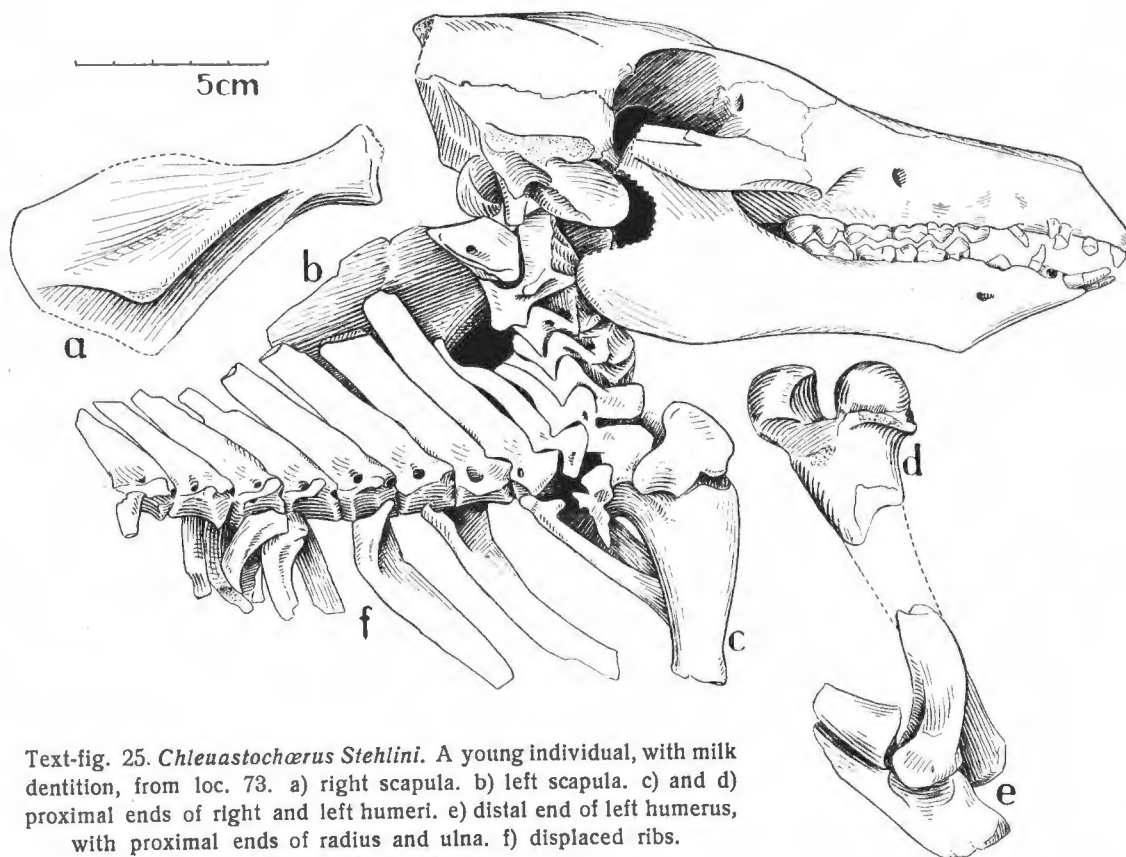
Text-fig. 24. *Chleuastochærus Stehlini*. Two right upper third molars from loc. 49, showing variation in size of talon. In a) the talon is unusually well developed, in b) it is little more than a posterior cingulum. Natural size.

As already stated, the dentition of *Chleuastochærus* is easily derivable from that of a *Palæochærus*: the third molars have become longer, stouter teeth, m^3 developing a talon, m_3 enlarging its talonid; the third incisors in both jaws are reduced and almost functionless, probably in correlation with the development of the curious snout region; the upper canines have broadened without lengthening, a process which in the males has reached an almost grotesque extreme. These dental characters point to the derivation of *Chleuastochærus* from some primitive, probably Asiatic, *Palæochærus*-like form along quite different lines from those on which the known species of the European Middle Miocene *Hyotherium* developed out of the European *Palæochærus*, although in some respects the two are in an equivalent stage of evolution. In *Hyotherium* the upper canines not only broadened but at the same time developed longer roots; the anterior premolars became elongated and compressed (*Hyotherium Scæmmeringii*), or enlarged and robust, losing the division into two of the main cusp of p_4 (*H. simorreense*).

B. The Skeleton of *Chleuastochærus*.

1. A young individual from locality 73.

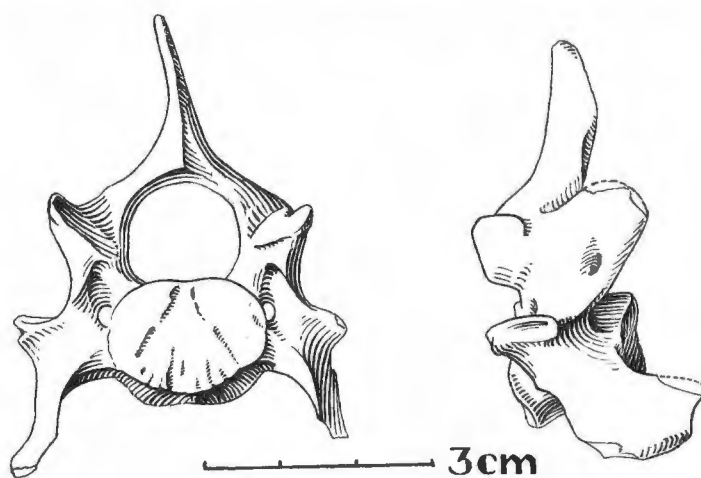
Text-fig. 25 represents part of the skeleton of a very young pig from locality 73. The bones are all rather crushed, the skull perhaps least so. Skull and vertebral column



Text-fig. 25. *Chleuastochærus Stehlini*. A young individual, with milk dentition, from loc. 73. a) right scapula. b) left scapula. c) and d) proximal ends of right and left humeri. e) distal end of left humerus, with proximal ends of radius and ulna. f) displaced ribs.

One half natural size.

were apparently fossilised nearly in the position in which they lay when the animal died. The right scapula, displaced in the drawing, lay across the anterior end of the vertebral column, its glenoid surface behind and below the disarticulated head of the right humerus. The left scapula may be seen in the drawing behind the neural spines of the anterior thoracic vertebræ, with its glenoid end lying close to the tympanic region of the skull. The two ends of the left humerus were also found, together with the still articulated proximal ends of the radius and ulna. So far as can be made out from so young and crushed a specimen all the parts of the skeleton other than the skull agree in structure with those of *Sus*.



Text-fig. 26. *Chleuastochærus Stehlini*. Anterior and lateral views of cervical vertebra from loc. 43. Natural size.

The slight differences in the transverse processes and cervical ribs of the neck vertebræ appear on close examination to be due to crushing and breakage: this is confirmed by an isolated cervical vertebra from locality 43₁, which is of the normal *Sus* pattern (text-fig. 26).

In the skull, the milk dentition is still in place: the tips of the permanent lower canine and third upper incisor may be seen pushing through the jaw. The milk canines are minute, pointed teeth with long, slender roots projecting far from the alveoli. There is as yet no trace of the characteristic supra-canine arch, nor is the prezygomatic shelf yet conspicuous.

2. Manus and pes.

i) Manus with radius and ulna from locality 12 (text-fig. 28).

ii) Crushed pes from locality 49 (text-fig. 27).

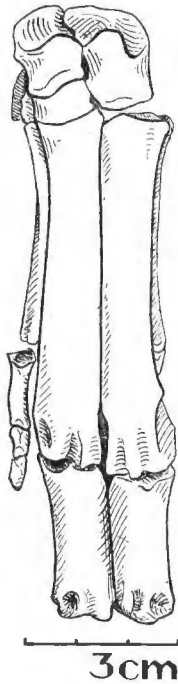
The central metapodials of both fore and hind feet are short and plump compared with those in *Sus* and *Potamochoerus*, but the lateral digits are strikingly slender in proportion to the central pair, and in the hind foot also strikingly shorter.

Noticeable in the carpus are:

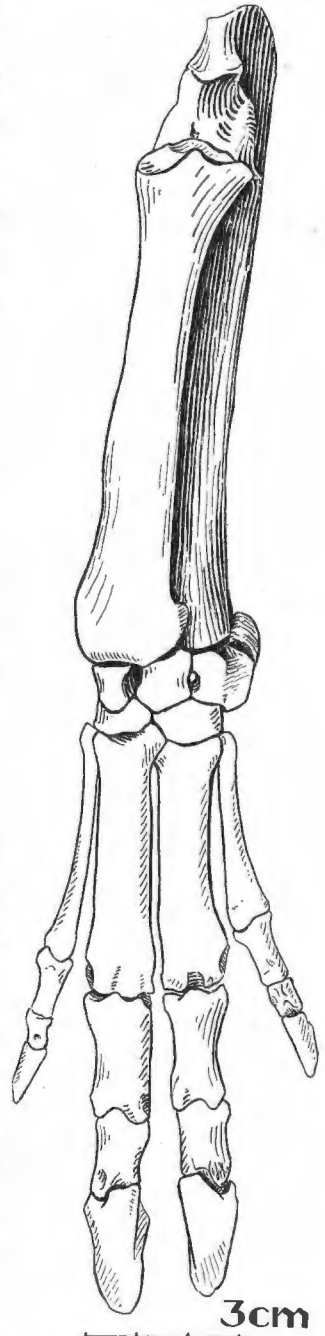
a) the large size of the process on the distal end of metacarpal III, articulating with the unciform and interlocking with metacarpal IV: this process is so wide that it nearly separates magnum from unciform.

b) The obtuseness of the angle between that surface of the unciform which articulates with the interlocking process of metacarpal III and that surface which articulates with metacarpal IV: in *Sus* this ventro-medial corner of the unciform is much more nearly rectangular, *i. e.* the arrangement of unciform and magnum in relation to metacarpals III and IV is much more nearly "serial".

c) The apparent absence on the unciform and lunar of the more proximal of the pair of facets by which in *Sus* these two bones articulate with one another, (*i. e.* the facets which in *Sus* lie above the foramen that pierces the carpus between these two bones).



Text-fig. 27.
Chleuastochærus Stehlini. Crushed left pes from loc. 49. Two thirds natural size.



Text-fig. 28. *Chleuastochærus Stehlini*. Left manus, radius and ulna from loc. 12. Two thirds natural size.

III. Variation in CHLEUASTOCHÆRUS.¹

In the last section of this paper I have tried to show that *Chleuastochærus* is a clearly defined new genus of pig. The next question that arises is whether there is more than one species of this genus represented in the *Lagrelius* collection.

In the attempt to separate species from species within a genus each type of animal needs to be treated differently. Different life habits must be taken into consideration, not only differences in structure. Among Carnivores, for instance, it is not uncommon to find several species of one and the same genus frequenting identically the same neighbourhood. In this case each species will probably have its own peculiar environment, — one preying on larger game, one on smaller, one a tree climber, and so on, — and, since the order as a whole is an unspecialised one, each species is able to cope with its own particular environment without differing very much from any of the others; and again owing to this lack of specialisation, none of the species are so firmly wedded to their own environment that they cannot wander away from it in one locality and seek it in another. Thus not only may several species of the same genus of Carnivores live side by side in the same locality, but these identical species may at the same time range over a very wide area of country outside this locality.

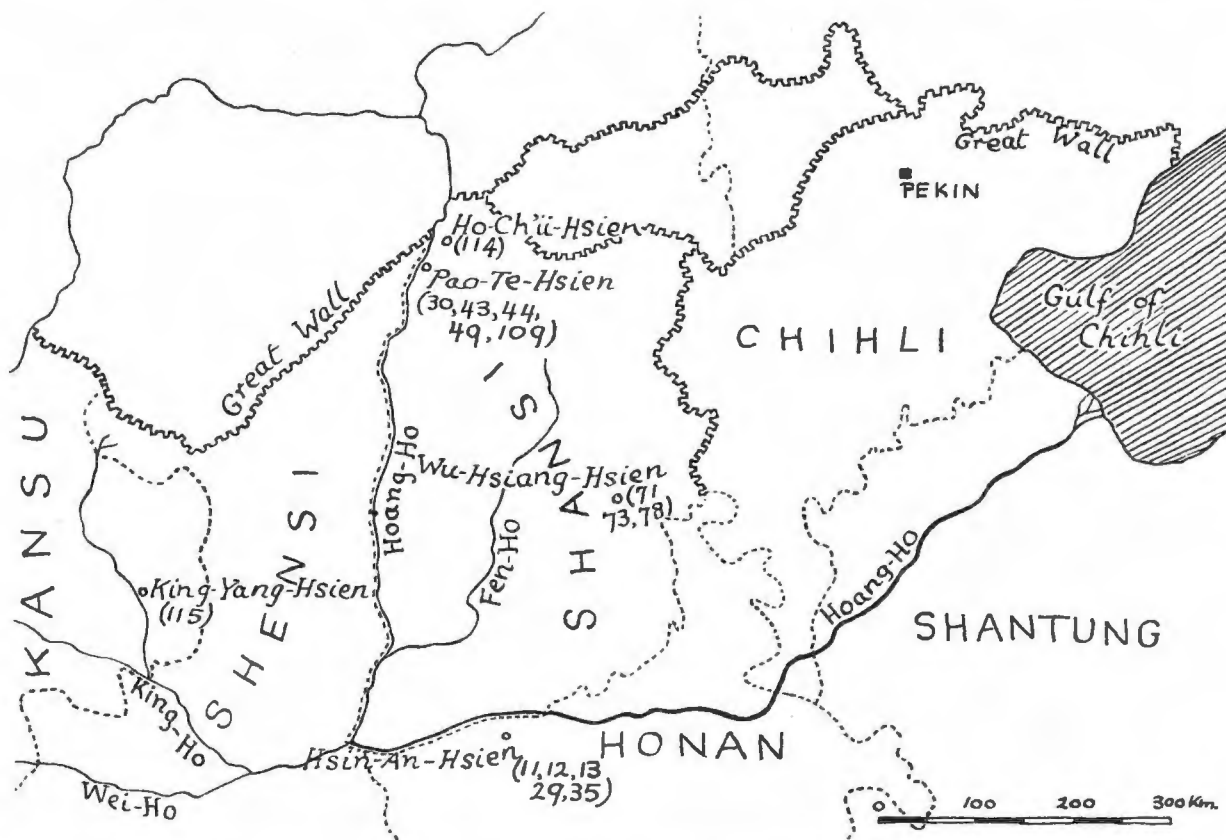
The distribution of the different species of Carnivora from the Chinese *Hipparion* fauna, as set forth by ZDANSKY in his "Jungtertiäre Carnivoren Chinas",² seems to fall in line with these general principles. For instance, he lists two species of *Parataxidea*, two of *Melodon*, two of *Machairodus*, two of *Metailurus*, and no less than four of *Ictitherium*, as all found in the Pao-Te-Hsien district within 5 kilometers of each other; and one or two of these species are according to him found 300 miles (500 kilometers) further south in Honan as well.

In seeking to distinguish possible species of *Chleuastochærus*, we must expect to find a different kind of distribution. It seems probable that this small pig lived in little communities or "sounders" like modern wild pig. Each community would probably have been confined to one more or less limited region, and would there have lived a life practically identical with that of the community in the neighbouring region. We should not expect to find any mingling of species in the same locality. More distant communities, perhaps living under slightly more or slightly less favourable food conditions, we should expect to differ a little in size and proportions. The further apart two

¹ This section has been completed and partially remoulded with the help of my brother, Dr. E. S. PEARSON of the Biometric Laboratory, University College, London. He is not, however, in any way responsible for its shortcomings.

² O. ZDANSKY, "Jungtertiäre Carnivoren Chinas", Pal. Sinica, Ser. 2. Vol. 2. Fasc. 1. 1924.

communities lived the greater are these differences likely to have been, owing to the greater environmental differences and the smaller chance of any interbreeding taking place. There might of course in some places be definite geographical barriers, isolating the pigs of one region from those of another and favouring differentiation into distinct local races or even distinct species, but in the case of the Chinese *Hipparion* fauna we have no reason to suppose that there were any barriers that pigs could not cross.



Text-fig. 29. Sketch map of N. W. China showing typical *Hipparion* fauna localities in which pigs were found.

Turning now to a study of the actual *Chleuastochærus* material we find that the specimens in the *Lagrelius* collection come mainly from four districts in Northern China (see map, text-fig. 29):

1. The district of Pao-Te-Hsien in N. W. Shansi. (Localities 30, 43, 44, 49 and 109, all of which are shown by Zdansky's map¹ of the region to lie within an area of five square kilometers).

¹ O. ZDANSKY. "Fundorte der Hipparion-Fauna um Pao-Te-Hsien in N. W. Shansi". Bull. Geol. Surv. China, No. 5. 1923.

2. The district of Wu-Hsiang-Hsien in S. E. Shansi, about 200 miles south-east of Pao-Te-Hsien. (Localities 71, 73, 78.)

3. The district of Hsien-An-Hsien in N. Honan, about 100 miles south of Wu-Hsiang-Hsien. (Localities 12, 13, 29, 35.)

4. The district of King-Yan-Hsien in E. Kansu, 270 miles south-west of Pao-Te-Hsien and 300 miles west of Wu-Hsiang-Hsien. (Locality 115.)

By far the greater part of the material was collected in the Pao-Te-Hsien neighbourhood and from locality 49. We are not sure that all the specimens from this locality were strictly contemporaneous, but there seems reason to believe that they were approximately so¹. If so, we can obtain from them a very fair idea of the degree of individual variation existing between members of a species living in the same locality and constituting what the statistician would call a "homogeneous population". We can then compare this pig population with the pigs coming from more distant localities, in order to find out whether the differences are in this case much greater than those within the population from locality 49, and if so whether they are sufficiently great to call for the recognition of separate species.

To obtain an accurate idea of the variability of a population the statistician tells us that we need to study very large samples of it, samples consisting of several hundred individuals. The palæontologist can rarely obtain such samples and has therefore to be content with less exact results. He has, as it were, only a few small pieces of the picture to look at, and has to guess at the rest from that. His uncertainty will probably be considerable, but every small additional piece of the picture that he can lay hands on will help to decrease this uncertainty. That is to say, that if he cannot get hold of big samples of a population he must take the biggest that he can get.

The largest sample of a *Chleuastochærus* population is from locality 49, but the material is of a varied nature. There are no absolutely complete skulls: the skulls lack different parts in different specimens, and some specimens consist solely of fragments of jaws with a few teeth. In order to deal in as large numbers as possible it is therefore necessary to choose those characters most commonly preserved and at the same time easily measurable. Such characters are the length and

¹ ZDANSKY'S plan of locality 49 (loc. cit.) shows that the fossils from that locality were found in five "pockets" at the end of one short lateral passage, and that the chamber excavated to gain access to the "pockets" was only three meters wide. The height of this particular chamber is not recorded, but in the Pao-Te-Hsien neighbourhood in general the "pockets" of *Hipparion* fauna fossils had an average size of 5 to 2 cubic meters (ZDANSKY, loc. cit. p. 72), while the passages leading to the chambers were less than a meter high (ZDANSKY p. 77). It is thus clear that all the *Chleuastochærus* specimens from loc. 49 must have been found extremely close together, and improbable that the animals represented, even if not absolutely contemporaneous, lived at periods sufficiently remote from each other for the race to have changed in the intervals.

Table I. Length and breadth measurements, and the length-breadth indices of upper molars of *Chleuastochærus* from locality 49.

M ¹			M ²			M ³		
L	B	$\frac{L}{B} \times 100$	L	B	$\frac{L}{B} \times 100$	L	B	$\frac{L}{B} \times 100$
11.3, 11.6	12.6	90, 92	16.0, 15.7	14.6, 14.8	110, 106	22.0, 21.6	15.3	144, 141
13.2	12.0	110	15.6	13.8, 14.1	113, 111			
14.3	12.7, 12.5	113, 114	17.4	14.6, 14.3	119, 122	23.5	15.9	148
			16.0	13.8, 14.0	116, 114	22.4, 21.5	14.5, 14.2	154, 151
14.3	12.4, 12.7	115, 113	17.0	14.7, 15.0	116, 113	24.6	15.5	159
13.8	11.8, 11.6	117, 119	17.7	13.2	134	20.8	14.2, 14.5	146, 143
12.8	12.0	107	15.1	14.3, 14.0	106, 108	21.6, 21.5	14.7	147, 146
15.1, 15.4	12.9	117, 119	18.8	15.4, 15.1	122, 125			
12.4	12.0	103						
			16.5	14.0	118			
12.9	12.3	105						
12.8	11.7, 11.5	109	16.1, 16.0	14.0	115, 114	20.8, 19.3	14.3, 14.2	145, 136
			16.6	13.9	119	21.3, 19.6	14.3, 14.2	147, 138
14.2	13.3	107	18.5	15.5	119	c. 24.0	15.8	152
14.0	12.3	114	16.5	13.7	120	21.0	14.5	145
			17.0	14.7	116	19.0	16.0	119
12.9	12.0	108	15.2	13.7	111			
14.7	12.4	119	17.3	14.6	118	21.0	15.0	140
						20.5	15.0	137
			17.1	15.0	114			
13.2	12.2	108	16.3	13.9	117			
13.2	12.2	108						
15.5	13.2	117						
[13.4]	[13.1]	[102]	[16.3]	[15.8]	[103]			

Note a. Where two numbers are given with a comma between them the number to the left of the comma refers to the tooth in the left maxilla, that to the right of the comma to the tooth in the right maxilla. Where only a single number is given, either the tooth was present on one side only, or the tooth of either side gave the same measurement.

Note b. The specimen whose measurements stand in brackets at the bottom of the list came from loc. 109 and was accidentally included with those from loc. 49 in calculating the means etc. of Table IV. Its measurements lie so close to these means, however, as to make no perceptible difference to the results; the localities also are very near to one another.

breadth of the molar teeth, and these I have measured in all possible cases, calculating also the indices of length to breadth ($\frac{\text{length}}{\text{breadth}} \times 100$). In *Tables I* and *II* these measurements and indices are listed for locality 49. The length measurements were taken antero-posteriorly across the middle line of the tooth from where it touched the one

Table II. Length and breadth measurements and the length-breadth indices of lower molars of *Chleuastochærus* from locality 49.

M ₁			M ₂			M ₃		
L	B	$\frac{L}{B} \times 100$	L	B	$\frac{L}{B} \times 100$	L	B	$\frac{L}{B} \times 100$
12.0	8.8	136	15.0, 15.3	11.2, 11.0	134, 139	c. 25.0	12.2	205
12.9	10.4	124	16.0	13.0	123	27.6, 25.5	13.7, 13.5	201, 189
14.0	9.8	143	16.7	12.5	134	25.0	13.4	187
13.6	10.3	132	17.4	12.4	140	26.6	13.7	194
12.6	8.6	147	14.4	10.7	135	20.5	11.1	185
c. 14.0	10.5	133	17.5	13.0	135			
14.4, 14.0	9.8, 9.6	147, 146	16.6	12.1	137	26.0	13.2	197
13.7	9.2	149	16.0	11.5	139	23.2, 22.5	12.4	187
13.6	9.8	139	16.8	11.9	141	25.5	13.0	196
13.4, 13.9	9.9, 9.6	135, 145	16.8	12.3, 12.4	137, 135	25.7	12.9	199
13.0	10.0	130	16.7	12.2	137	22.6, 23.0	13.0, 12.8	174
13.2	9.2, 9.3	143, 142	16.1	11.1, 11.2	145, 144		12.3	
13.5	9.1	148	16.4	11.5	143	c. 26.0	12.3, 12.4	c. 211
						26.5	12.2	217
13.7	9.3	147	15.9	11.7	136	25.0	13.0, 13.2	192
14.7	9.6	153						
14.8	9.3	159	17.0	11.6	147	23.2	12.1	192

in front to where it touched the one behind; in the case of the third molars the hinder end of the tooth was taken as lying in the plane passing through the posterior surface of talon or talonid, and perpendicular to the grinding surface of the anterior part of the tooth. The breadth measurements were in all cases taken across the broadest part of the crown in the anterior part of the tooth, — that is to say in a plane cutting the anterior pair of roots.

Since many palæontologists may not be conversant with the simple statistical methods that I have used in dealing with these measurements, it will perhaps be as well to give here a short explanation of them, showing how the results were obtained. In this explanation I have made use of the extremely lucid little "Primer of Statistics" (Adam and Charles Black, 1909) by W. P. and E. M. ELDERTON, and to Miss E. M. ELDERTON herself, of the Biometric Laboratory, University College, London, I am very particularly indebted for checking the greater part of my mathematics, correcting several errors, and giving me much helpful information and advise.

Variation in the breadth of the third upper molar. Let us take as an example variation in the breadth of the third upper molar. There are 13 specimens from loca-

Table III. Example showing calculation of Mean, Standard Deviation and Coefficient of Variation in case of breadth of M³.

Breadth of M ³	Deviation from Mean	Square of Deviation	
15.3	+ 0.3	0.09	$\frac{195.0}{13.0} = 15.00 = \text{Mean}$
15.9	+ 0.9	0.81	
14.5	- 0.5	0.25	$\frac{5.0}{13.0} = 0.3846 = \text{Average of squares of deviations.}$
15.5	+ 0.5	0.25	
14.2	- 0.8	0.64	$\sqrt{0.3846} = 0.620 = \text{Standard Deviation.}$
14.7	- 0.3	0.09	
14.3	- 0.7	0.49	$\frac{100 \times 0.620}{15.00} = 4.13 = \text{Coefficient of Variation.}$
14.3	- 0.7	0.49	
15.8	+ 0.8	0.64	
14.5	- 0.5	0.25	
16.0	+ 1.0	1.00	
15.0	0.0	0.00	
15.0	0.0	0.00	
<u>195.0</u>		<u>5.00</u>	

lity 49 in which this measurement can be taken. Their breadths are listed in the first column of *Table III*.

The mean of these breadths, — that is to say the average breadth obtained by adding them all together and then dividing by 13, — is 15 millimeters. In the second column are listed the deviations of each individual molar from this mean; the + or — sign in front of each number shows whether the deviation is in a direction greater or less than the mean. In the third column these deviations are squared, (the + and — signs thus being eliminated,) and the squares are added up. Again the result is divided by 13. The square root of the number thus obtained is termed by statisticians the *standard deviation*, and provides a measure of the dispersion or variability about the mean. In this case the standard deviation is approximately 6 mm.

If it be desired to compare the variation in one group with that in another a direct comparison of the standard deviations may be misleading, if the absolute measure of size differs considerably in the two groups.¹ What is required is a comparison of *relative* variability, and this is obtained by using the ratio:

$$\frac{\text{standard deviation}}{\text{mean}} \times 100,$$

called the *coefficient of variation*, which gives the measure of variation as a percentage of the average value of the character.

¹ For example, as measured by the standard deviation, the breadth of an elephant's skull has a far wider variation than that of a mouse, but it is the relative rather than this absolute variability that is of possible biological interest!

Now it has to be remembered that these results for mean, standard deviation, and coefficient of variation have been obtained from measurements on a very small sample of the population, — only thirteen individuals. How far are they likely to hold good for the total population could we measure it? If we could collect a second sample of the population, and make the same measurements and calculations, how nearly should we find the results to be the same?

This we cannot tell exactly, but statistical theory based upon the laws of probability enables us to draw certain inferences, provided always that we are justified in assuming the sample to be a fair or random one. When the mean, standard deviation, or coefficient of variation are estimated from a sample, the reliability of the estimate is measured conventionally by the so-called *probable error*. This measure is based upon the variation observed within the sample and upon the size of the sample, since the reliability of the estimate naturally increases with the number of individuals upon which it is based. Broadly speaking, it is *rather unlikely* that the estimate based on a sample should differ from the true value for the population sampled by more than two or three times this probable error; it is *very unlikely* that it differs from the true value by as much as four times the probable error.

Using the appropriate formulæ,¹ we may again illustrate the method by taking the breadth measurements of third upper molars from locality 49. If P. E. be the probable error, m be the mean, n the number of molars measured, s the standard deviation, and v the coefficient of variation, then, since $n = 13$, $m = 15.00$, $s = 0.62$, $v = 4.13$:

$$\text{P. E. } m = 0.187 \times 0.62 = 0.12$$

$$\text{P. E. } s = 0.132 \times 0.62 = 0.08$$

$$\text{P. E. } v = 0.132 \times 3.79 = 0.50$$

The mean may now be written in conventional manner as 15.00 ± 0.12 , the standard deviation as 0.62 ± 0.08 , and the coefficient of variation as 0.13 ± 0.50 .

By a method essentially similar to that employed in Table III but a little easier to use,² the means, standard deviations, and coefficients of variation, with their pro-

¹ Formulæ for the probable errors used, and tables to assist in their calculation, may be found in "Tables for Statisticians and Biometricians", edited by KARL PEARSON, Cambridge University Press, 2nd ed. 1924. The formulæ are given on p. xxii, the constants in Tables V and VI.

² If the mean does not prove to be a whole number as it did in the example given, it is laborious to use it when determining the deviations of the variates and the squares of these deviations. In this case the same results may be obtained by taking any whole number close to the mean and reckoning the deviations from this. Then the following formula may be used for calculating the standard deviation:

$$(\text{Standard Deviation})^2 = \frac{\text{Sum of squares of deviations}}{\text{Total number of variates}} - (\text{Mean deviation})^2.$$

Table IV. Variation in *Chleuastochærus* molars from locality 49.¹

Measurement or Index	Number of Variates	Mean	Standard Deviation	Coefficient of Variation
Lm ¹	18	13.6 ± 0.2	1.0 ± 0.1	7.4 ± 0.8
Lm ²	19	16.7 ± 0.1	1.0 ± 0.1	5.8 ± 0.6
Lm ³	13	21.7 ± 0.3	1.5 ± 0.2	6.9 ± 0.9
Bm ¹	18	12.4 ± 0.1	0.5 ± 0.1	3.8 ± 0.4
Bm ²	19	14.4 ± 0.1	0.7 ± 0.1	4.7 ± 0.5
Bm ³	13	15.0 ± 0.1	0.6 ± 0.1	4.1 ± 0.5
$\frac{L}{B} m^1 \times 100$	18	109.4 ± 1.1	6.9 ± 0.8	
$\frac{L}{B} m^2 \times 100$	19	116.1 ± 1.0	6.4 ± 0.7	
$\frac{L}{B} m^3 \times 100$	12	144.2 ± 1.9	9.5 ± 1.3	
Lm ₁	16	13.6 ± 0.1	0.7 ± 0.1	5.3 ± 0.6
Lm ₂	15	16.4 ± 0.1	0.8 ± 0.1	5.0 ± 0.6
Lm ₃	14	24.9 ± 0.3	1.8 ± 0.2	7.2 ± 0.9
Bm ₁	16	9.6 ± 0.1	0.5 ± 0.1	5.6 ± 0.7
Bm ₂	15	11.9 ± 0.1	0.7 ± 0.1	5.5 ± 0.7
Bm ₃	15	12.7 ± 0.1	0.7 ± 0.1	5.3 ± 0.6
$\frac{L}{B} m_1 \times 100$	16	141.7 ± 1.5	9.0 ± 1.1	
$\frac{L}{B} m_2 \times 100$	15	137.4 ± 0.9	5.5 ± 0.7	
$\frac{L}{B} m_3 \times 100$	14	195.6 ± 1.9	10.8 ± 1.4	

¹ The calculations have only been recorded to one place of decimals, since it is doubtful if the original measurements were strictly accurate to a tenth of a millimeter. The probable errors so given provide a rough indication of the reliability of the means, standard deviations, and coefficients of variation.

able errors, have been obtained for all the molar measurements; they are set out in Table IV.

It will be noticed that no coefficients of variation are given for the length-breadth indices; this is because, in the case of an index, the standard deviation may be used directly for purposes of comparison: to calculate a further coefficient of variation would be superfluous and meaningless.

From this table it appears that the most variable of the characters taken are the lengths of the first upper molar, the third upper molar and the third lower molar. This variability of the third molars would certainly be anticipated from the very ob-

vious differences in the shape and size of their talons and talonids, (see p. 30 above), and also because it is very difficult to take their length measurement consistently. That the first upper molar should be so variable in length might not be suspected from an inspection of the jaws themselves, but is probably due to the very worn condition of these teeth in the older skulls, where they may be ground down below the level of the enamel, and hollowed out at either end by the tooth in front and the tooth behind pressing into them.

Variation in the molar measurements of a homogeneous human population. Before comparing with the population of locality 49 the far fewer individuals of *Chleuastochærus* from the other localities, it may be of value to make a comparison of the molar measurements of this Suid population with similar measurements taken from a larger sample of a "homogeneous" human population — a collection of skulls of the Naqada race from the prehistoric cemeteries of Upper Egypt, dated at approximately between 7000 and 5000 B. C.¹ The number of teeth available for each measurement in this case varied from 26 to 69, thus considerably more than are available in the case of *Chleuastochærus*. Furthermore it was possible to separate male skulls from female and left molars from right, which it has not been possible to do with the Suid material. The molar measurements of the female skulls are usually slightly smaller than those of the male skulls: in the case of the upper molars this difference may average half a millimeter, but in the case of the lower molars it is rarely more than a tenth of a millimeter. If the differences are equally small in the case of *Chleuastochærus* the results will not be materially affected by a mixture of the sexes.

A comparison of the columns in *Tables IV* and *V*, listing the coefficients of variation, shows that while the range of variation in the molars of the human population is approximately from 5 to 12.5, with an average coefficient of about 7, that in the pig population is from 3.5 to 7.5, with an average of about 5.5: that is to say, the Naqada molars are on the whole slightly more variable than the *Chleuastochærus* molars. This may possibly be because human molars are degenerating organs and therefore more variable, or it may be that the pig material from locality 49 represents an even more homogeneous group than the Naqada skulls.

For further comparison a few other coefficients of variation may be given, for

¹ See C. D. FAWCETT, *Biometrika*, vol. 1. 1901—1902, p. 408, Cambridge University Press. "A Second Study of the Variation and Correlation of the Human Skull, with Special Reference to the Naqada Crania". These skulls are stored in the Biometric Laboratory, University College, London. The hitherto unpublished measurements of the molar teeth, and the calculations of the means, standard deviations and coefficients of variation, were made by the members of that laboratory, to the Director of which I am indebted for the permission to make use of them here.

As regards the homogeneity of this collection of skulls see FAWCETT, *loc. cit.* p. 424.

Table V. Variation in the molar measurements and indices of a homogeneous human population (Naqada race). Males and females, right and left jaws, are treated separately. The number of teeth measured in each case varies from 26 to 69.

[From the archives of the Biometric Laboratory, University College, London.]

	M e a n						S t a n d a r d d e v i a t i o n						C o e f f i c i e n t o f v a r i a t i o n					
	♂		♀		♀		♂		♀		♂		♀		♂		♀	
	Right	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right	Left	Right	Left
Lm ¹	10.2 ± 0.06	10.2 ± 0.07	9.9 ± 0.06	9.9 ± 0.06	0.7 ± 0.05	0.7 ± 0.05	0.8 ± 0.05	0.7 ± 0.05	0.7 ± 0.05	0.7 ± 0.05	0.7 ± 0.05	0.7 ± 0.04	0.7 ± 0.04	6.4 ± 0.44	7.6 ± 0.49	7.5 ± 0.46	7.4 ± 0.45	7.4 ± 0.45
Lm ²	9.8 ± 0.07	9.7 ± 0.06	9.4 ± 0.06	9.6 ± 0.06	0.7 ± 0.05	0.7 ± 0.04	0.7 ± 0.04	0.7 ± 0.04	0.7 ± 0.04	0.7 ± 0.04	0.7 ± 0.04	0.7 ± 0.04	0.7 ± 0.04	7.6 ± 0.50	7.3 ± 0.45	7.6 ± 0.44	7.6 ± 0.44	7.6 ± 0.44
Lm ³	8.9 ± 0.07	9.3 ± 0.08	8.9 ± 0.09	8.7 ± 0.12	0.6 ± 0.05	0.6 ± 0.06	0.6 ± 0.06	0.6 ± 0.06	0.8 ± 0.06	0.8 ± 0.06	0.8 ± 0.06	1.0 ± 0.08	1.0 ± 0.08	6.7 ± 0.54	6.9 ± 0.59	9.1 ± 0.70	11.4 ± 0.96	11.4 ± 0.96
Bm ¹	11.5 ± 0.06	11.3 ± 0.05	10.9 ± 0.05	10.9 ± 0.05	0.6 ± 0.04	0.6 ± 0.04	0.6 ± 0.04	0.6 ± 0.04	0.6 ± 0.04	0.6 ± 0.04	0.6 ± 0.04	0.6 ± 0.04	0.6 ± 0.04	5.0 ± 0.34	5.4 ± 0.34	5.7 ± 0.49	5.7 ± 0.34	5.7 ± 0.34
Bm ²	11.5 ± 0.07	11.5 ± 0.05	11.0 ± 0.06	11.0 ± 0.05	0.7 ± 0.05	0.6 ± 0.04	0.6 ± 0.04	0.6 ± 0.04	0.7 ± 0.05	0.7 ± 0.04	0.7 ± 0.04	0.7 ± 0.04	0.7 ± 0.04	6.2 ± 0.40	5.6 ± 0.34	6.2 ± 0.36	5.9 ± 0.34	5.9 ± 0.34
Bm ³	11.0 ± 0.10	11.2 ± 0.10	10.4 ± 0.11	10.4 ± 0.16	0.9 ± 0.07	0.8 ± 0.07	0.8 ± 0.07	0.8 ± 0.07	1.0 ± 0.08	1.0 ± 0.08	1.0 ± 0.08	1.3 ± 0.11	1.3 ± 0.11	8.0 ± 0.63	7.1 ± 0.62	9.9 ± 0.75	12.7 ± 1.1	12.7 ± 1.1
$\frac{L}{B}m^1 \times 100$	89 ± 0.6	90 ± 0.6	91 ± 0.5	91 ± 0.6	5.7 ± 0.40	6.6 ± 0.42	6.6 ± 0.42	6.6 ± 0.42	6.4 ± 0.39	6.4 ± 0.39	6.4 ± 0.39	7.4 ± 0.45	7.4 ± 0.45					
$\frac{L}{B}m^2 \times 100$	86 ± 0.7	85 ± 0.6	86 ± 0.5	87 ± 0.5	7.6 ± 0.50	6.8 ± 0.41	6.8 ± 0.41	6.8 ± 0.41	6.0 ± 0.34	6.0 ± 0.34	6.0 ± 0.34	5.8 ± 0.34	5.8 ± 0.34					
$\frac{L}{B}m^3 \times 100$	81 ± 0.7	84 ± 0.6	86 ± 0.7	84 ± 1.0	6.5 ± 0.52	5.2 ± 0.45	5.2 ± 0.45	5.2 ± 0.45	6.6 ± 0.51	6.6 ± 0.51	6.6 ± 0.51	8.1 ± 0.67	8.1 ± 0.67					
Lm ₁	10.6 ± 0.08	10.6 ± 0.09	10.6 ± 0.07	10.6 ± 0.08	0.7 ± 0.06	0.7 ± 0.06	0.7 ± 0.06	0.7 ± 0.06	0.6 ± 0.05	0.6 ± 0.05	0.6 ± 0.05	0.7 ± 0.05	0.7 ± 0.05	6.2 ± 0.52	7.0 ± 0.58	6.0 ± 0.47	7.0 ± 0.52	7.0 ± 0.52
Lm ₂	10.7 ± 0.09	10.6 ± 0.10	10.7 ± 0.06	10.5 ± 0.07	0.9 ± 0.07	0.9 ± 0.07	0.9 ± 0.07	0.9 ± 0.07	0.7 ± 0.05	0.7 ± 0.05	0.7 ± 0.05	0.7 ± 0.05	0.7 ± 0.05	8.4 ± 0.63	8.3 ± 0.64	6.2 ± 0.43	6.3 ± 0.46	6.3 ± 0.46
Lm ₃	10.4 ± 0.08	10.6 ± 0.10	10.5 ± 0.10	10.4 ± 0.12	0.6 ± 0.06	0.8 ± 0.07	0.8 ± 0.07	0.8 ± 0.07	0.8 ± 0.07	0.8 ± 0.07	0.8 ± 0.07	0.9 ± 0.08	0.9 ± 0.08	6.0 ± 0.54	7.9 ± 0.69	7.5 ± 0.59	8.3 ± 0.79	8.3 ± 0.79
Bm ₁	10.5 ± 0.07	10.5 ± 0.07	10.4 ± 0.06	10.3 ± 0.06	0.6 ± 0.05	0.6 ± 0.05	0.6 ± 0.05	0.6 ± 0.05	0.5 ± 0.04	0.5 ± 0.04	0.5 ± 0.04	0.5 ± 0.04	0.5 ± 0.04	5.4 ± 0.44	5.6 ± 0.47	5.2 ± 0.41	5.2 ± 0.38	5.2 ± 0.38
Bm ₂	10.2 ± 0.07	10.2 ± 0.07	10.2 ± 0.05	10.1 ± 0.05	0.7 ± 0.05	0.6 ± 0.05	0.6 ± 0.05	0.6 ± 0.05	0.5 ± 0.04	0.5 ± 0.04	0.5 ± 0.04	0.5 ± 0.04	0.5 ± 0.04	6.6 ± 0.50	6.1 ± 0.47	5.1 ± 0.35	5.2 ± 0.39	5.2 ± 0.39
Bm ₃	9.9 ± 0.07	9.9 ± 0.07	9.9 ± 0.07	9.8 ± 0.08	0.6 ± 0.05	0.6 ± 0.05	0.6 ± 0.05	0.6 ± 0.05	0.6 ± 0.05	0.6 ± 0.05	0.6 ± 0.05	0.6 ± 0.06	0.6 ± 0.06	6.0 ± 0.53	6.1 ± 0.52	5.8 ± 0.45	6.3 ± 0.59	6.3 ± 0.59
$\frac{L}{B}m_1 \times 100$	102 ± 0.7	101 ± 0.8	102 ± 0.5	103 ± 0.6	5.8 ± 0.49	6.4 ± 0.53	6.4 ± 0.53	6.4 ± 0.53	4.3 ± 0.34	4.3 ± 0.34	4.3 ± 0.34	6.1 ± 0.45	6.1 ± 0.45					
$\frac{L}{B}m_2 \times 100$	105 ± 0.7	104 ± 0.7	105 ± 0.5	105 ± 0.5	6.6 ± 0.49	6.5 ± 0.49	6.5 ± 0.49	6.5 ± 0.49	5.0 ± 0.35	5.0 ± 0.35	5.0 ± 0.35	5.0 ± 0.37	5.0 ± 0.37					
$\frac{L}{B}m_3 \times 100$	105 ± 0.6	107 ± 0.7	106 ± 0.7	106 ± 0.9	4.9 ± 0.44	5.4 ± 0.47	5.4 ± 0.47	5.4 ± 0.47	5.8 ± 0.51	5.8 ± 0.51	5.8 ± 0.51	6.8 ± 0.63	6.8 ± 0.63					

characters of the human skull other than those of the dentition, some again for the Naqada population, others for other populations also regarded as homogeneous.¹

1. *Skull Coefficients.*

<i>Naqada race.</i>		♂	♀
Length of skull		3.17	3.14
Breadth of skull		3.29	3.45
Horizontal circumference		2.54	2.27
Length of palate		6.49	7.41
Breadth of palate at m ²		9.29	8.55
Height of mandible		9.93	8.47

	<i>Other races.</i>		Breadth of skull	
	Length of skull ♂	♀	♂	♀
Bavarian peasants.....	3.37	3.57	3.89	3.39
Whitechapel English	3.44	3.66	3.55	3.78
Parisian French	3.97	3.65	4.21	3.67
Aino.....	3.20	3.08	2.76	2.68

2. *Miscellaneous Coefficients.*

	<i>Cambridge Undergraduates.</i>		♂	♀
Stature			3.64	3.79
Weight.....			10.72	11.05
Strength of pull.....			15.58	16.73
Eye-sight (right eye).....			33.25	34.74

From these data we can gain an idea of the extent to which variation occurs in a diversity of measurable characters within several types of homogeneous population, and we may conclude that the amount of variation in the molar teeth of our material from locality 49 is no more than we might expect to find in a mammalian population of comparable homogeneity.

Comparison of *Chleuastochoerus* material from different localities.

Let us suppose, then, that the teeth from locality 49 belonged to animals forming a homogeneous group, and enquire whether teeth from other localities appear to differ

¹ See FAWCETT, loc. cit. and K. PEARSON. "The Chances of Death" vol. 1., chap. VIII, 1897, in both of which many other coefficients will be found.

from these significantly or not. The problem is essentially one that must be dealt with by what the statistician calls the methods of *small samples*. In some cases we have only single specimens to base our judgments on, and even the material from the Wu-Hsiang-Hsien district (localities 71, 73 and 78, see *Tables VI* and *VII*) is barely sufficient to justify the calculation of mean measurements. Had there been, for example, even fifty specimens from locality 49 and fifty from locality 73 it might have been possible

Tables VI and *VII*. Length and breadth measurements, and the length-breadth indices of *Chleuastochærus* molars from the Wu-Hsiang-Hsien district.

M ¹			M ²			M ³		
L	B	$\frac{L}{B} \times 100$	L	B	$\frac{L}{B} \times 100$	L	B	$\frac{L}{B} \times 100$
13.7, 13.5	12.4	111	14.5	13.5	107	17.5	13.3	132
11.7	11.7	100	13.4	12.8	105	17.3	13.2	131
13.4	12.2	110						
12.9	11.7	110	14.8	13.8	107			
10.8	10.8	100	13.1	12.1	108	15.1	12.8	118
						19.3	14.2	136

M ₁			M ₂			M ₃		
L	B	$\frac{L}{B} \times 100$	L	B	$\frac{L}{B} \times 100$	L	B	$\frac{L}{B} \times 100$
13.9	9.2, 9.5	151						
12.5	8.8	142						
13.3			15.3			23.7	12.0, 11.9	198
13.8	8.8	157						
* { 13.4	{ 8.5	{ 158	{ 14.7	{ 9.7	{ 152	{ 21.8	{ 10.9	{ 200
{ 13.2	{ 8.6	{ 154	{ 14.4	{ 9.9	{ 146	{ 21.6	{ 10.8	{ 200
12.5	9.3	134	15.9	10.8, 11.1	147	24.6	12.0	205
13.5	9.3	145						
						22.0	11.1	198
12.2	8.0	153	13.7	10.0	137	22.0	10.9	202
12.4	8.9	139	14.2	10.4	137	22.9	11.2	205
			[14.3]**	[10.2]	[140]	[21.9]	[10.8]	[203]

* Of these two bracketed specimens the measurements of only the first were included in calculating the means, since they appear to have been opposite jaws of the same individual.

** The specimen whose measurements are placed in square brackets comes from locality 71; in calculating the means it has been included with the rest, all of which come from locality 73.

to form a very definite opinion as to the difference between the pig populations of these two localities. But though it is difficult in the present case to reach certain conclusions, there are several very suggestive results to be obtained from an analysis of our material.

(i) *Comparison of teeth from locality 49 with those from locality 73.*

We may commence by asking whether the difference between the average meas-

Tables VIII and IX. Comparison of means for loc. 73 with those for loc. 49.

	Means for Loc. 49 + 109	Means for Loc. 73	P
Lm ¹	13.56 (18)*	12.50 (5)*	0.064
Lm ²	16.68 (19)	13.95 (4)	under 0.001
Lm ³	21.71 (13)	17.30 (4)	under 0.001
Bm ¹	12.89 (18)	11.76 (5)	0.024
Bm ²	14.38 (19)	13.05 (4)	0.008
Bm ³	15.00 (13)	13.87 (4)	under 0.001
$\frac{L}{B}m^1 \times 100$	109.4 (18)	106.0 (5)	0.334
$\frac{L}{B}m^2 \times 100$	116.1 (19)	106.8 (4)	0.012
$\frac{L}{B}m^3 \times 100$	144.2 (12)	129.2 (4)	0.016

	Means for Loc. 49	Means for Loc. 73+71	P
Lm ₁	13.57 (16)*	13.06 (9)*	0.009
Lm ₂	16.35 (15)	14.68 (6)	under 0.001
Lm ₃	24.92 (14)	22.70 (9)	0.010
Bm ₁	9.60 (16)	8.85 (8)	0.004
Bm ₂	11.61 (15)	10.22 (5)	under 0.001
Bm ₃	12.70 (15)	11.27 (7)	under 0.001
$\frac{L}{B}m_1 \times 100$	141.7 (16)	147.2 (8)	0.179
$\frac{L}{B}m_2 \times 100$	137.4 (15)	142.2 (5)	0.129
$\frac{L}{B}m_3 \times 100$	195.4 (14)	201.3 (7)	0.206

* Numbers in brackets denote number of variates upon which means were calculated.

ures (means) for these two localities is more than might be expected to arise through the chance fluctuations of sampling, having regard to the variation observed within the two samples. If two samples be drawn from the same population, and the average measures, μ_1 and μ_2 , be found for each, then it needs no wide experience to tell us that μ_1 will not generally be exactly equal to μ_2 . If we imagine several sets of two samples taken and compared, the difference $\mu_1 - \mu_2$ will vary from pair to pair, being sometimes positive and sometimes negative. The amount of this variation depends upon the size of the samples and upon the variation of the character from individual to individual in the population sampled.

There is a statistical test for small samples¹ which indicates whether it is likely, having regard to the observed variation in the two samples, that the difference between their means could have arisen from the chance fluctuations of sampling, or whether it is more probable that the samples have been drawn from populations having significantly different means. This test has been applied to the difference between the mean values of the eighteen molar measurements and indices for localities 49 and 73+71. The results are indicated under the heading P in the final column of *Tables VIII* and *IX*. This quantity P provides in each case a measure of the probability that differences as great or greater than those observed would arise from mere chance fluctuation between two samples of the same population. For example, in comparing the breadth of first lower molars, for which a sample of 16 from locality 49 gives a mean of 9.60, and a sample of 8 from locality 73 a mean of 8.85, the test tells us that, having regard to the observed variation within these samples, so great a difference would only be expected to arise, in sampling from a single population, in about 4 trials out of 1000. Thus, in spite of the smallness of the samples, we may justly infer it to be unlikely that the third lower molars were of the same average length in the two groups of pigs to which our specimens belonged. Still more are we justified in inferring a significant difference between the two groups when we find that for *all* the measures except those of shape (i. e. the indices) P has a very low value: a value representing odds of from 10 to 1 to more than 1000 to 1 against the differences merely being due to the chances of sampling.

The pigs from localities 73+71 then, judging from their molar teeth, were on the average almost certainly smaller animals than those from locality 49.

(ii) *Comparison of teeth from locality 49 with those from the remaining localities.*

¹ R. A. FISHER, *Metron* vol. V. 3. 1925, p. 8.

In the case of the remaining localities, except for locality 12, we have only single specimens on which to base our comparisons (see *Table X*). From locality 12 we

Table X. Length and breadth measurements, and the length-breadth indices, of *Chleuastochærus* molars from the remaining localities.

	<i>Pao-Te-Hsien</i>			<i>Hsin-An-Hsien</i>					<i>King-Yan-Hsien</i>
	Loc. 30 ₉	Loc. 43 ₁	Loc. 44	Loc. 29	Loc. 12	Loc. 12	Loc. 35	Loc. 13	Loc. 115
Lm ¹		11.9		12.2	12.6	10.4			10.5
Lm ²		14.7	14.2	14.0	15.0	13.6			13.8
Lm ³		18.4	20.4, 19.0	17.7		19.6	18.2		16.2
Bm ¹		10.9, 10.5		11.1					10.3
Bm ²		12.3	14.0	13.2	14.2	13.0			11.9
Bm ³		13.2	14.1, 13.6	13.7	14.2	14.3	12.5		12.2
$\frac{L}{B}m^1 \times 100$		109, 113		110					102
$\frac{L}{B}m^2 \times 100$		120	101	106	106	104			116
$\frac{L}{B}m^3 \times 100$		139	145, 140	129		137	146		133
Lm ₁	14.3					11.4			
Lm ₂	16.7			15.0		14.6		15.9	
Lm ₃				20.8		22.8		22.9	
Bm ₁	9.4					8.8			
Bm ₂	10.9			10.1		10.2			
Bm ₃				10.3		11.3			
$\frac{L}{B}m_1 \times 100$	152					130			
$\frac{L}{B}m_2 \times 100$	153			149		143			
$\frac{L}{B}m_3 \times 100$				202		202			

have two specimens, (the mandible from this locality is probably associated with the older of the two skulls); these will be treated separately, as their mean measurements would clearly be of no value. In comparing these isolated specimens with the group from locality 49 the test used above cannot be employed. Two methods remain: a) to note whether the single measurements lie outside the range of corresponding measurements for the locality 49 group, b) to compare the deviation of these single measurements from the means of the locality 49 group with the standard deviations

of that group. This second method is the more satisfactory, and statistical theory tells us that it is *rather* unlikely that an individual measurement will deviate from the mean measurement of a population from which it has been drawn by more than twice the standard deviation in that population, while it is *extremely* unlikely that it will deviate by as much as three times this standard deviation. It must of course be remembered that the standard deviations available are only those estimated from the small sample of pigs from locality 49. We must not therefore draw too definite conclusions from the ratios of deviation to standard deviation, but the analysis is suggestive, and, in the absence of further material, the best that can be done.

Table XI shows the result of applying this test to our *Chleuastochærus* material. In the first column is the list of standard deviations (s) of all the mean measurements for locality 49 (repeated from *Table IV*). In the remaining columns there are listed for each of the remaining localities: i) the deviation (d) of each measurement from the corresponding mean measurement of locality 49; ii) the ratio ($\frac{d}{s}$) of this deviation to the corresponding standard deviation of locality 49. Every value of ($\frac{d}{s}$) greater than 2 is placed in square brackets to indicate that the deviation is probably a significant one. It is clear that the greater the number of bracketed values for any one specimen, the more unlikely is it that the individual represented by this specimen could have belonged to the same group as those from locality 49.

Tested in this way it is the pig from locality 115 in Eastern Kansu that appears to differ most from the locality 49 group: since this has a very well developed supra-canine arch and its molar teeth are well worn, it was clearly a full grown male, which makes its small size all the more striking. Of the five pigs from Northern Honan, three — from localities 29, 35 and 12 — were smaller animals than we should be likely to find among the locality 49 population; two others — from locality 13 and a second individual from locality 12 — might have been included in such a population. Finally, of the three pigs from localities in North Western Shansi, within 5 kilometers of locality 49 itself, one (locality 30) might very well have belonged to the locality 49 population, another (locality 43) is extremely unlikely to have done so, the third (locality 44) is perhaps rather unlikely.

It may be noted that just as in the case of the specimens from locality 73 the differences are in the *size* of the molar teeth (i. e. the length and breadth measurements), rather than in their *shape* (i. e. the indices). Only three of all the indices listed differ by more than twice the standard deviation from those of the locality 49 group of pigs.

Table XI. Comparison of *Cheuastocherus* molars from other localities with those from loc. 49. [s = standard deviation for loc. 49, d = deviation from mean of loc. 49].

	Pao-Te-Hsien						Hsin-An-Hsien						King-Yan-Hsien	
	Loc. 49	Loc. 30 ₂	Loc. 43 ₁	Loc. 44	Loc. 29	Loc. 12	Loc. 12	Loc. 35	Loc. 13	Loc. 115				
	s	d	d	d	d	d	d	d	d	d	d	d		
Lm ¹	1.0		-1.7		-1.4	-1.4	-1.0	-1.0	-3.2	-3.1	-3.1	-3.1		
Lm ²	1.0		-2.0	-2.5	-2.7	-2.7	-1.7	-1.8	-3.1	-2.9	-2.9	-3.0		
Lm ³	1.5		-3.3	-1.3, -2.7	-0.9, -1.8	-4.0			-2.1	-5.5	-5.5	-3.7		
Bm ¹	0.5		-1.5, -1.9	-3.2, -4.0		-1.3			-2.1	-2.1	-2.1	-4.5		
Bm ²	0.7		-2.1	-0.4	-0.6	-1.2	-0.2	-0.3	-1.4	-2.5	-2.5	-3.7		
Bm ³	0.6		-1.8	-0.9, -1.4	-1.5, [-2.3]	-1.3	-0.8	-1.3	-0.7	-2.8	-2.8	-4.5		
L m ¹ × 100...	6.9		-0.2, +3.9	0.0, +0.6	+0.5	+0.5				-7.5	-7.5	-1.1		
L m ² × 100...	6.4		+3.4	-14.7		-10.0	-10.5	-1.6	-12.3	-0.1	-0.1	0		
L m ³ × 100...	9.5		-4.8	+0.5, -4.5	+0.1, -0.5	-15.0				-11.4	-11.4	-1.2		
Lm ₁	0.7	+0.7				-1.4	-1.7	-1.7	-2.2	-0.5	-0.5	-0.6		
Lm ₂	0.8	+0.3				-4.1	-2.3	-2.3	-1.8	-2.0	-2.0	-1.1		
Lm ₃	1.8								-2.1					
Bm ₁	0.5	-0.2				-1.8	-2.8	-2.8	-0.8	-1.5	-1.5			
Bm ₂	0.7	-1.0				-2.4	-3.5	-3.5	-1.7	-2.6	-2.6			
Bm ₃	0.7								-1.4	-2.1	-2.1			
L m ₁ × 100...	9.0	+10.4	+1.2			+11.1	+2.0	+2.0	-12.2	+1.0	+1.0			
L m ₂ × 100...	5.5	+15.8	[+2.9]			+6.3	+0.6	+0.6	+5.7	+0.6	+0.6			
L m ₃ × 100...	10.8								+6.2					

Discussion. We have next to consider whether these statistically detected differences can be interpreted in terms of the current biological conceptions of "species", "sub-species", "local varieties", etc. Are the differences in any one case sufficiently great to be regarded as of even "sub-specific" value? In the first section of this paper it was stated that there were no obvious morphological differences, only size differences, between the skulls of *Chleuastochærus* in the *Lagrelius* collection. The relative sizes of the molar teeth studied in this section appear to afford a convenient guide to these size differences in the skulls, so that we may fairly base our conclusions on the molar measurements alone.

It has been argued above (pp. 33 to 35) that on *a priori* grounds we should expect to divide our material, if at all, into four local varieties, sub-species, or possibly even species: i) from the Pao-Te-Hsien district, ii) from the Wu-Hsiang-Hsien district, iii) from the Hsin-An-Hsien district, iv) from the King-Yan-Hsien district. But we have just shown that within the first of these districts the two pigs from localities 43 and 44 appear to be differentiated from those of the locality 49 group, although locality 43 is only 3 kilometers from locality 49, and locality 44 only 1 kilometer. In explanation of this there are three possibilities:

1. The specimen from locality 44 and still more so that from locality 43 do after all chance to be extreme deviations from the locality 49 mean, although the chance is an unlikely one.

2. The material from localities 43 and 44 is not contemporaneous, even approximately, with that from locality 49. There seems no way of deciding this point at present.

3. Our twenty or thirty¹ pigs from locality 49 are not after all a fair sample of the population of the district. Perhaps they all belonged to one large herd, comparable with a herd of peccaries rather than with a sounder of modern wild pig². The members of this herd may have been closely inbred and therefore have varied in size around their own particular mean, which would have differed slightly from the mean for the total population of the district. This possibility again cannot be substantiated, for we know too little of the way in which the animals met their death, whether simultaneously or no.

¹ Unfortunately the association of mandibles with skulls has not been maintained. Except in a very few cases it now seems impossible to be sure of any such association. Therefore it is uncertain how many individuals are represented.

² It may be noted that of the individuals from locality 49 at least three were undoubtedly boars, one a very old boar, the other two younger but with well worn first molars. Further sexing of the material is not possible: no other male upper canine regions are preserved and the lower canines show such a wide variation in size that no certain line can be drawn between male and female.

The pigs from all the southern localities, as far as we can judge from our few specimens, were about as much smaller than the average locality 49 pig as were the two pigs from localities 43 and 44; there seems clearly no reason for regarding them as of different species from these two, although they come from such widely different districts.

The single pig from Eastern Kansu appears to have been still smaller than was usual in the more eastern districts, and if we were sure that it was a typical member of the population to which it belonged we might well regard this population as a local variety of the genus. Our specimen may, however, have chanced to be an exceptionally small individual, as is apparently the case with one of those from locality 73, which in some of its measurements (Lm^2 , Lm^3) is even smaller.

Conclusions.

1. There is no evidence that more than one species of *Chleuastochærus* existed in the Chinese *Hipparion* fauna.

2. The variation in size of teeth among the animals of the largest group (that from locality 49) is not greater, judged by the coefficient of variation, than we should expect to find in a sample from a single homogeneous race. When, however, we compare the mean measurements of this group with those of the only other large group (that from localities 71 and 73), the latter are, without doubt, significantly smaller. This suggests a conclusion which is to some extent confirmed by the measurements of single individuals from other localities: that the average size of the pigs populating one neighbourhood differed from that of those populating another. The information as to the relative geological age of the specimens is, however, inadequate.

3. As has been emphasised repeatedly, the material so far collected is not adequate to allow any clear definition of these local varieties, or even to establish for certain their existence. The statistical analysis is none the less worth while because it at least shows how such inadequate data *cannot* yield definite conclusions as regards species and varieties, and at the same time points to the only sound method of procedure as further evidence becomes available. That this should be clearly recognised is of considerable importance, for it should serve as a warning against the crude methods of species-making generally current in systematic palæontology.

IV. "SUS" (MICROSTONYX) ERYMANTHIUS ROTH and WAGNER?

Localities: 114 south, 114 north, 44?

From locality 114 come the following fragments which I think may be referred provisionally to "*Sus*" *erymanthius* ROTH and WAGNER, recently given by Pilgrim the new generic name *Microstonyx*.¹

a) From locality 114 south. A somewhat crushed mandible lacking the ascending rami, (text-fig. 30).

Length of symphysis, measured along outer surface of mandible to alveolus of first incisor — circ. 8.5 cm.

LM ₁ * 17.5 mm. (left), 18.5 mm. (right)	BM ₁ * 16.5 mm. (left), 15.8 mm. (right)
LM ₂ 26.5 " " 26.4 " "	BM ₂ 21.4 " " 20.8 " "
LM ₃ 44.0 " " 45.7 " "	BM ₃ 23.0 " " 23.3 " "

$$\frac{L}{B}M_1 \times 100 = 106 \text{ (left), } 117 \text{ (right)}$$

$$\frac{L}{B}M_2 \times 100 = 124 \text{ " } 127 \text{ "}$$

$$\frac{L}{B}M_3 \times 100 = 191 \text{ " } 196 \text{ "}$$

b) From locality 114 north. Part of the right ramus of the mandible of a young individual with dm₂ to m₁ (Pl. III, text-figs. 3 and 4).

LDm₄ 26.5 mm.

LM₁ 21.7 mm. BM₁ 14.7 mm. $\frac{L}{B}M_1 \times 100 = 148$

c) From locality 114 north. Two very battered fragments of right and left maxillæ, possibly belonging to the same individual, with p⁴ to m² and p⁴ to m³ respectively. In the latter m³ is not yet cut.

LM ¹ 20.0 mm. (left), 20.0 mm. (right)	BM ¹ —
LM ² 29.0 " " 28.5 " "	BM ² 25.0 mm. (left), 25.0 mm. (right)

$$\frac{L}{B}M^2 \times 100 = 116 \text{ (left), } 114 \text{ (right)}$$

(Owing to the crushing, these measurements are not very exact.)

These fragments are all strikingly similar in colour and in matrix to material from the typical Pikermi *Hipparion* fauna. Were they mixed with a number of *Microstonyx*

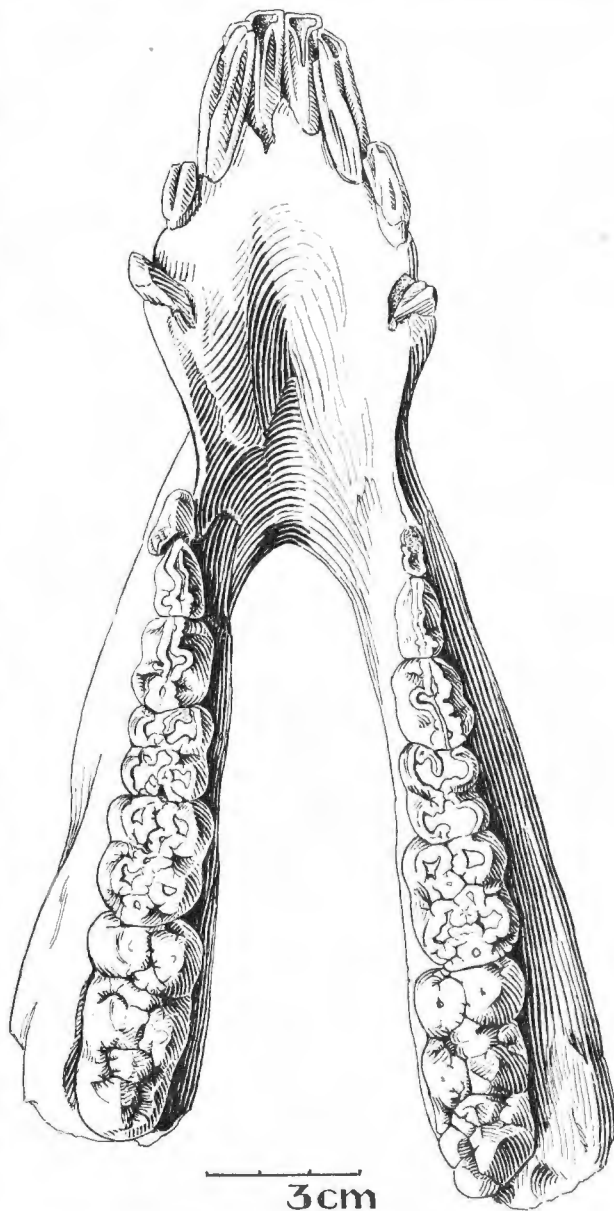
¹ G. E. PILGRIM. "The Fossil Suidæ of India" Pal. Ind. N. S. vol. VIII, 1926 pp. 7 to 8.

* These measurements were taken in the manner already described for *Chleuastochærus*, see above pp. 36 and 37.

erymanthius jaws from the Pikermi beds it would be hardly possible to distinguish them. The lower incisor teeth are similar to those of *Microstonyx*, and the canine teeth are of the typically insignificant peg-like type. The main cusp of p_4 is cleft at the tip into twin summits, which lie lateral to one another just as in *Microstonyx*, *Hyotherium Sæmmeringii*, or *Palæochoærus*.

A decided difference from the Pikermi *Microstonyx* appears to lie in the very much shorter symphysis and premolar region of the Chinese mandible, and in their different shape. Measurement shows however that the premolars themselves are not significantly shorter, and a closer examination of the uneven surface of the mandible suggests that, prior to mineralisation, when in a soft condition, the anterior end was pressed back on the hinder end in such a way as to cause impaction of the bone and thus shortening and distortion of the jaw. Owing to this impaction, the left second premolar has been shifted backwards so that its somewhat crushed hinder end lies lateral to the anterior end of the third premolar; the right second premolar has retained its normal position.

Small differences in the pattern of the Chinese teeth compared with those from Pikermi are perhaps to be found in: (a) the greater breadth posteriorly of p_3 , which has a small additional fold or cusplet on its labial surface: (b) the presence of a well developed style in the middle of the lingual side of m_2 between the protocone and "hypocone". It is possible, however, that similar characters may sometimes occur as variations in Pikermi material. The immature mandibular fragment — (b) on p. 52 — compares extremely well with a similar fragment from Pikermi (British Museum, No. 9079).



Text-fig. 30. *Microstonyx erymanthius?* Mandible with impacted symphysis from loc. 114 south. Two thirds natural size.

Tables XII and XIII. Length and breadth measurements, and length-breadth indices of molar teeth of *Microstonyx erymanthius* from Pikermi.

M ¹			M ²			M ³		
L	B	$\frac{L}{B} \times 100$	L	B	$\frac{L}{B} \times 100$	L	B	$\frac{L}{B} \times 100$
22.9	20.5	112	28.6	26.5	108	39.3	28.0	140
			30.8	25.0	123			
23.2	19.3	120						
22.4	20.9	107	30.5	26.6	115			
						39.9	26.3	152
						40.6	26.5	153
						42.0	29.8	141
21.3			28.1	25.7, 25.3	109, 111	41.6	26.6	156
			26.2			41.0	27.9	147
20.3	19.4	105	27.0	24.0	113			
19.6			27.3	24.4, 24.7	112, 111	43.2	26.5, 27.7	163, 156
22.5	19.8	114	29.6	24.9	119	38.7	26.4	147
21.9			27.9	26.4	106	42.3	27.2, 28.1	156, 151
19.5	18.0	108						
21.9	19.1	115						
22.3	20.3	110	28.5	26.0	110			
21.9	20.2	108	29.6	26.1	113	38.1	27.9	137
20.5	19.9	103	29.0	25.2	115			
21.6	20.0	108	29.0	25.0	116			

M ₁			M ₂			M ₃		
L	B	$\frac{L}{B} \times 100$	L	B	$\frac{L}{B} \times 100$	L	B	$\frac{L}{B} \times 100$
19.3	14.3	135	27.5	17.9	154	41.2	21.1	195
			28.0	18.0	156	40.2	20.8	193
21.2	14.5, 14.3	147, 148						
18.5	15.9	116	25.3	20.2	125	41.2	21.8	189
			29.2	21.6	135	46.7	23.8	196
24.6	16.0	154						
20.8	14.2	147						
			30.5	21.9	139			
			29.0	20.9	139			
						40.2	22.7	177
19.0			27.8	20.3	137	46.0	24.7	186
19.8	14.4	138	25.8	18.8	137	39.3	21.8	181
			27.0	21.0	129	43.7, 44.2	23.0	190, 192
			25.1	19.9	126	40.2	21.9	184
20.7			29.3	22.2	132	45.4	24.9	182
22.1	15.5	143	27.6	19.8	139	43.2	22.2	195
19.6	15.2	129	25.2	19.3	131	43.5	21.2	205
22.6	15.5	146						
22.0	17.0	129	29.0	21.4	136	41.7	23.5	177
			27.8	19.3	144	48.1	22.5	214
						43.5	22.3	195

Molar measurements compared with those of Pikermi material. A comparison of the molar measurements of the Chinese *Microstonyx* with those given in Tables

XII and XIII for *Microstonyx* material from Pikermi, shows a very close agreement, considering how far apart the two animals lived. The means, standard deviations and coefficients of variation for the Pikermi material are given in *Table XIV*.

The first molar on the left side of the adult mandible from locality 114 is shorter than any I have so far measured from Pikermi, but that on the right side is the same length as an unusually short molar from Pikermi. This shortness is partly due to the teeth being very worn, and scooped out at either end where p_4 in front and m_2 behind are impacted into them; this naturally also affects the length-breadth index of these first molars, making it a very low number compared with the Pikermi indices, especially as the breadth is rather greater than the Pikermi mean breadth for m_1 .

In the young mandibular fragment from locality 114, where the first molar is only just cut and the second molar not in place behind it, the former gives a length

Table XIV. Variation in *Microstonyx erymanthius* molars from Pikermi.

Measurement or Index	Number of Variates	Mean	Standard Deviation	Coefficient of Variation
Lm ¹	14	21.6 ± 0.2	1.1 ± 0.1	5.2 ± 0.7
Lm ²	13	28.6 ± 0.2	1.3 ± 0.2	4.5 ± 0.6
Lm ³	10	40.7 ± 0.3	1.6 ± 0.2	3.9 ± 0.6
Bm ¹	11	19.8 ± 0.2	0.8 ± 0.1	3.8 ± 0.5
Bm ²	12	25.5 ± 0.2	0.8 ± 0.1	3.2 ± 0.5
Bm ³	10	27.3 ± 0.2	1.1 ± 0.2	3.8 ± 0.6
$\frac{L}{B}m^1 \times 100$	11	110.0 ± 0.9	4.6 ± 0.7	
$\frac{L}{B}m^2 \times 100$	12	113.2 ± 0.9	4.7 ± 0.6	
$\frac{L}{B}m^3 \times 100$	10	149.1 ± 1.7	7.9 ± 1.2	
Lm ₁	12	20.9 ± 0.3	1.7 ± 0.2	8.1 ± 1.2
Lm ₂	15	27.6 ± 0.3	1.6 ± 0.2	5.8 ± 0.7
Lm ₃	15	42.9 ± 0.4	2.6 ± 0.3	6.0 ± 0.7
Bm ₁	10	15.3 ± 0.2	0.9 ± 0.1	5.7 ± 0.9
Bm ₂	15	20.2 ± 0.2	1.3 ± 0.2	6.4 ± 0.8
Bm ₃	15	22.5 ± 0.2	1.2 ± 0.1	5.3 ± 0.6
$\frac{L}{B}m_1 \times 100$	10	138.2 ± 2.2	10.5 ± 1.6	
$\frac{L}{B}m_2 \times 100$	15	137.2 ± 1.5	8.5 ± 1.0	
$\frac{L}{B}m_3 \times 100$	15	190.7 ± 1.7	9.8 ± 1.2	

measurement slightly greater than that of the Pikermi mean but well within the standard deviation, while the breadth measurement is slightly less than the Pikermi mean but again within the standard deviation; the length-breadth index, though greater than the Pikermi mean, is also within the standard deviation.

The length and breadth measurements of the second molars of the adult mandible fall within the standard deviation of the Pikermi mean, if the probable error in calculating the latter be allowed for in the case of the breadth of the tooth in the right jaw; the index, however, is again rather low, deviating from the Pikermi mean index by more than the standard deviation, though not by twice as much. The third molars of this mandible are both larger and broader than the Pikermi means but still fall within the standard deviations of these latter, and their indices also.¹

The maxillary fragments from locality 114 are in very bad condition, the teeth much worn and cracked, but the measurements, as far as they are worth anything, would again fall within the Pikermi series, except once more for the length of m^1 , which, like its fellow of the lower jaw, is rather short.

Conclusions. Better material of the Chinese *Microstonyx* may show that it was of a sufficiently distinct race from the Pikermi pig to be given a different specific name. Until then I have thought it best to refer it to the classical *erymanthius* species, as have been the similar pigs from Samos, Maragha and other *Hipparion* faunæ.

An immature skull of *Microstonyx erymanthius*??

Locality 44.

From locality 44 comes part of the skull of a young pig with milk dentition (see text-fig. 31), so young that it is very hard to say whether it would have really developed into a *Microstonyx* or no.

M^1 , the only certain link between so young a skull and its adult condition, gives the following measurements:

LM¹ 20.5 mm. BM¹ 18.0 mm. (left), 17.5 mm. (right)

$\frac{L}{B}M^1 \times 100 = 113$ (left), 117 (right)

This affords no real clue, as these measurements might fall within the range of variation of either the larger *Microstonyx erymanthius* or the rather smaller *Propot-*

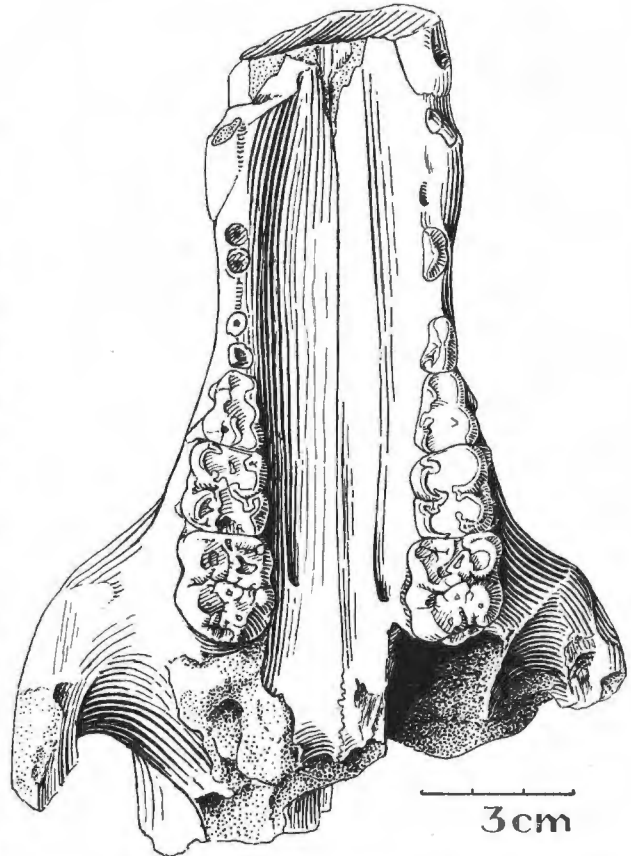
¹ The talonids of these third molars are markedly different from one another in pattern, although on the right and left sides of the same mandible; this affords a clear demonstration of how little weight can be placed on such differences when comparing one species of pig with another.

amochærus hyotherioides (see section V), the proportions of m^1 in these two pigs not being so different as those of the posterior molars.

After comparing this fragment with immature skulls of *Sus* and *Potamochærus* it seems to me that the evidence is on the whole in favour of its belonging to a *Microstonyx*. The milk canine is extremely small and feeble for so large an animal. The permanent canine is as yet entirely buried within the maxilla: in young *Potamochærus* skulls, where the cheek teeth are as much worn as these are, the permanent canine projects well out of its alveolus. In this skull there is a long diastema between the milk canine and the first premolar, and a second diastema between the latter and dm^2 : in *Sus* and *Potamochærus*, whether the first premolar is present or not, there is never a long gap between the milk canine and the cheek teeth.

I have also compared the Chinese specimen with an immature maxillary fragment from Pikermi, which however has unfortunately no canine, (British Museum No. 9061). All the teeth in this fragment are rather larger than those in the Chinese skull, but they appear to be of the same pattern; that the first premolar is absent here and present in the Chinese skull is not a very significant difference, since this tooth has been found in other specimens of *Microstonyx* and is a variable character in the modern genus *Potamochærus*. The slight prominence over the alveolar border of the maxilla posterior to the root of the deciduous canine has a very similar appearance in the two specimens.

It should be noted, however, that we have no evidence that *Propotamochærus hyotherioides* agreed closely with a modern *Sus* or *Potamochærus* in the degree of development of its milk canines and post-canine diastemata. Nor must one overlook the fact that the large isolated canine referred below (p. 59) to *Propotamochærus hyotherioides* comes from the same locality as the young skull.



Text-fig. 31. *Microstonyx erymanthius*? Young skull, with milk dentition, from loc. 44. Two thirds natural size.

V. Propotamochoerus hyotherioides SCHLOSSER.

Localities 49, 44, 66, Lu-Chia-Ling, Tan-Tsun.

Definitive characters (if all the fragments described below belong to this same species). A very large pig from the Lower Pliocene and possibly later Pliocene, characterised by stout cheek teeth of simple pattern. M^3 especially short and broad. P^1 very small with no diastema separating it from p^2 . P^2 and p^3 long. P_4 with main eusp cleft at summit into two small peaks placed one behind the other; talonid high, anterior cingulum inconspicuous. Lower canines large and "scrofic" in adult male.

Material.

a) Palate from locality 49 — the same locality as the greater part of the *Chleuastochærus* material. (Pl. IV, fig. 3.)

Width across palate at level of p^3	47 mm.
" " " " " " antero-internal roots of m^1	44 mm.
" " " " " " " " " " m^3	34.5 mm.
Length of dental series, p^2 to m^3 inclusive	123.5 mm.
" from p^3 to m^3 inclusive	110.0 mm.
" " m^1 to m^3 "	79.3 mm. (right), 80.3 mm. (left)
* LM^1 19.0 mm.	* BM^1 18.0 mm.
LM^2 24.5 mm.	BM^2 21.6 mm. (left), 22.2 mm. (right)
LM^3 35.5 mm. (left), 35.8 mm. (right)	BM^3 26.0 mm.

$$\frac{L}{B}M^1 \times 100 = 106$$

$$\frac{L}{B}M^2 \times 100 = 113 \text{ (left), } 110 \text{ (right)}$$

$$\frac{L}{B}M^3 \times 100 = 137 \text{ (left), } 138 \text{ (right)}$$

The posterior palatine foramina are opposite the gap between m^2 and m^3 . The infra-orbital foramen lies above the gap between p^4 and m^1 . The molars are all cut, but m^3 only just so, and m^1 and m^2 not yet much worn.

b) Fragment of left mandible, with p_4 to m_3 , also from locality 49, (Pl. IV, figs. 1 and 2). This makes so good a fit with the palate just described that there can be little doubt that it is of the same species, though since m_3 is only half cut and the anterior molars are barely worn at all, it cannot have belonged to the same individual. The molar measurements are as follows:

$$*LM_1 \text{ 18.5 mm.} \quad *BM_1 \text{ 12.0 mm.}$$

$$*LM_2 \text{ 24.4 mm.} \quad *BM_2 \text{ 15.6 mm.}$$

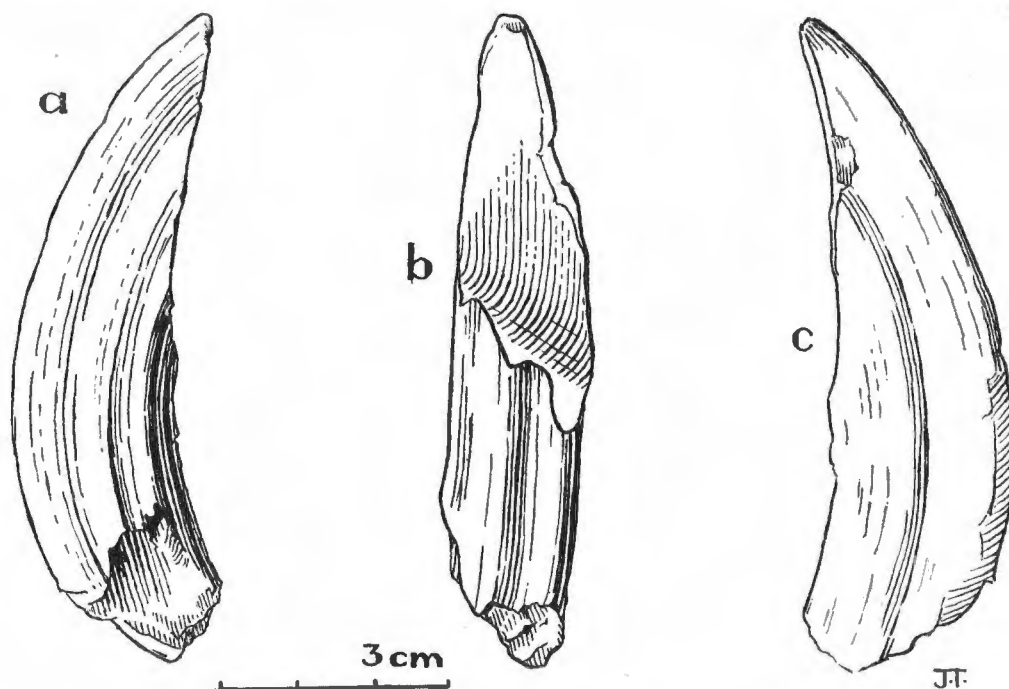
$$*BM_3 \text{ 18.6 mm.}$$

$$\frac{L}{B}M_1 \times 100 = 154$$

$$\frac{L}{B}M_2 \times 100 = 156$$

* These measurements were taken in the way that has already been described for *Chleuastochærus*, see pp. 36 and 37.

P_4 of this mandible gives conclusive evidence that this pig is not merely a smaller species of *Microstonyx*. The main cusp of this tooth is cleft at the tip, slightly but distinctly, and the twin summits thus formed are placed one behind the other, whereas in *Microstonyx* they lie side by side (or nearly so) and the cleft between them is much more marked, the tooth therefore being much fatter. The talonid also of this p_4 is higher in comparison with the main cusp than in *Microstonyx*.



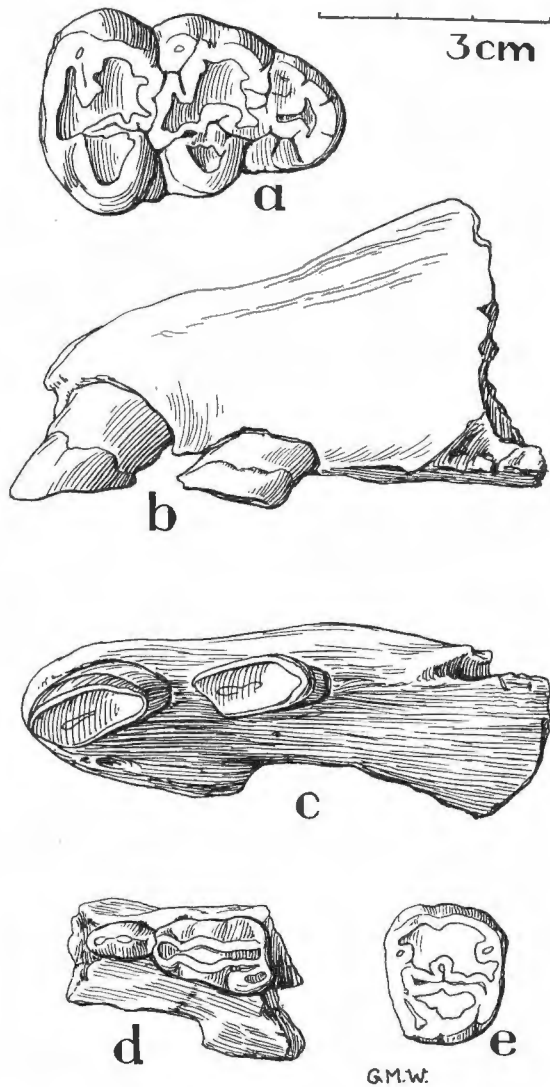
Text-fig. 32. *Propotamochærus hyotherioides*. Isolated lower left canine from loc. 44: a) labial view with shaded posterior surface in perspective; b) posterior, and c) lingual views. Natural size.

c) Further evidence of the existence in the Chinese *Hipparion* fauna of a large genus of pig other than *Microstonyx* with its reduced canines, is afforded by an isolated lower left canine from locality 44, a typical *Hipparion* fauna locality (text-fig. 32). This is of a type intermediate between the extreme "scrofic" and the "verrucose", and of a size suited to a pig with the palate and mandible just described.

Certain other material in the *Lagrelius* collection also appears to belong to this same large species, but is of less certain geological age, namely:

d) The hinder region of the snout of a large pig from Lu-Chia-Ling in the Chin-Hsien district of Shansi. Present are m^3 of either side, a broken right m^2 , and the roots of the other cheek teeth broken off at jaw level. The fragment is very heavy, the matrix being a hard purple-brown sandstone, while the bone is light brown in

colour and the teeth a pale grey-brown, so that the whole appearance is very different from that of most of the *Hipparion* fauna material described in this paper. An accompanying pencil note of Zdansky's, written probably a long time ago, says: "According to my opinion from strata younger than the *Hipparion* clay. I guess at Middle or Upper Pliocene".



The palate gives almost identical measurements with that from locality 49, but m^3 lacks the additional cusplet which there stands out so prominently postero-external to the metacone, with a projecting root of its own. The nasal and zygomatic regions of this skull are somewhat crushed, but the snout muscle origins seem to be of the *Sus* type; the preservation is too poor for a drawing to be worth while.

Width across palate at level of p^3	48.5 mm.
" " " " " " " " antero-internal roots of m^1	44.0 mm.
Width across palate at level of p^3 antero-internal roots of m^3	39.0 mm.
Length of dental series from p^3 to m^3 inclusive.....	123.5 mm.
Length of dental series from m^1 to m^3 inclusive	circ. 79.5 to 80.0 mm.
Lm^2	24.5 mm.
LM^3	37.2 (left), 39.0 (right) BM^3 25.0 (left), 25.3 (right)
$\frac{L}{B}M^3 \times 100 =$	149 (left), 154 (right)

Text-fig. 33. *Propotamochoerus hyotherioides*. Fragments of upper dentition, apparently of one individual, from Tan-Tsun in Shansi. Natural size. a) Right m^3 . b) and c) Fragment of left premaxilla, with i^1 , i^2 and part of alveolus of a small i^3 . d) Left p^1 and p^2 . e) P^4 .

The posterior palatine foramina are level with the middle of m^3 . The infra-orbital foramen lies above the gap between p^4 and m^1 .

e) From Tan-Tsun in the Yü-She-Hsien district of Shansi come the following fragments which apparently all belong to the upper jaw of one individual.

- i. A right m^3 , (text-fig. 33 a).
- ii. The posterior part of a left m^3 .
- iii. A p^4 , (text-fig. 33 e).

iv. A left p^1 and p^2 , with portion of alveolus for a large canine; p^1 is a very small tooth pressed closely against the anterior end of p^2 (text-fig. 33 d).

v. A fragment of left premaxilla with i^1 , i^2 and part of the alveolus of i^3 , (text-fig. 33 b and c).

vi. A fragment of right premaxilla with i^1 and the alveolus of i^2 .

All these teeth are in an advanced stage of wear; as far as size is concerned they may very well have belonged to the same species of pig as a), b) and c) above. The matrix in this case is a light brown sandstone, the bone grey-brown and the teeth grey-blue. As far as I know there is no information as to the geological age.

LM³ 39.6 mm. BM³ 26.5 mm.

$$\frac{L}{B}M^3 \times 100 = 149$$

f) Locality 66.

i. A very worn m^3 , (text-fig. 34 a).

LM³ 42.0 mm. BM 25.0 mm.

$$\frac{L}{B}M^3 \times 100 = 168$$

ii. An unworn m^2 .

LM² 28.3 mm. BM² circ. 23.5 mm.

$$\frac{L}{B}M^2 \times 100 = 120$$

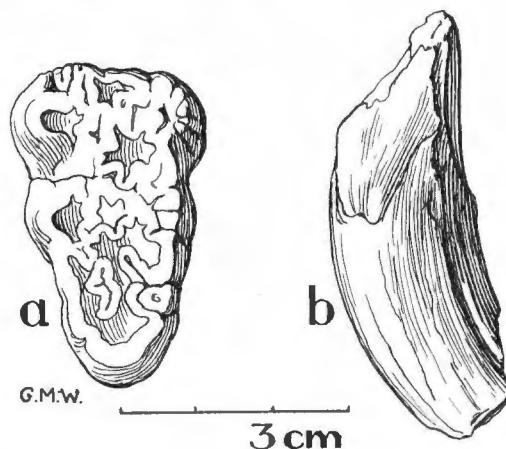
iii. A fragment of left maxilla with broken p^3 and the roots of p^4 and p^2 .

iv. A broken ♀ lower canine, (text-fig. 34 b).

All these again appear from their size to have belonged to the same species as a), b) and c) above, thus suggesting that this locality is really Pliocene and not Pleistocene (see ZDANSKY's doubts, Pal. Sin., Series C., vol. 5, 1927, p. 12).

Discussion.

SCHLOSSER distinguished two species among the molar teeth of large pigs from China described and figured by him in 1903¹. To the smaller of these he gave the name *Sus hyotherioides*, the other he simply called "*Sus n. sp. ind.*". The geological age of all these teeth is uncertain. With the kind per-



Text-fig. 34. *Propotamochoerus hyotherioides*. a) right m^3 , b) fragment of left lower canine of a female; from loc. 66. Natural size.

¹ MAX SCHLOSSER, "Die fossilen Säugethiere Chinas" Abh. der Königl. bayerischen Akad. d. Wissensch. Bd. 22, 1903, p. 92.

mission of Professors Schlosser and Broili, I have myself examined these molars in Munich, and see no reason why the larger should not have belonged to a *Microstonyx*, the smaller to the same species as the palate and mandible from locality 49, the measurements of which I have given above. I have therefore referred these latter to "*Sus*" *hyotherioides* SCHLOSSER, to avoid creating an entirely new name, but it must be remembered that pigs' molar teeth rarely give characters — other than the highly variable ones of size and proportions — which admit of their specific or even generic distinction. On the evidence of the premolar teeth, I have changed the generic name to *Propotamochærus* PILGRIM¹, though there are differences from the Indian species of that genus in the more scrofic pattern of the male lower canine and in the distinct division of the main cusp of p_4 ; (for further discussion see pp. 69 to 71 below).

MATTHEW and GRANGER in 1923² gave a photograph of the side view of a pig's skull from the Yen-Ching-Kao fissures, the fauna from which they believed to be Upper Pliocene. They suggested that this pig might be referable to SCHLOSSER's *Sus hyotherioides*. To give an idea of its size they compared the skull with that of a modern *Potamochærus*, stating only that its p^4 is larger and more complex. Judging from this comparison however, and from the magnification given on the photograph, their pig was markedly smaller than the pig from locality 49, and, since the molar teeth of the latter agree in size very well with SCHLOSSER's teeth, could hardly have belonged to SCHLOSSER's species. It would be interesting to have more information about this skull from the Upper Pliocene, because, while large pigs of the robust *Propotamochærus* type appear to have been characteristic of the earlier Pliocene, they seem to have disappeared before the Pleistocene, giving place to much smaller species of *Sus* resembling the modern Chinese wild pig.

VI. *SUS* sp. from Pleistocene and later deposits.

Localities 105, 106, 67, 61, I-Tu-Hsien, Nan-Shan.

Fragmentary material from the loess indicates that China in Pleistocene times was inhabited by species of *Sus* very little different from those to be found there today³.

¹ G. E. PILGRIM, "The Fossil Suidæ of India". *Pal. Indica* N. S. vol. VIII, 1926, p. 22.

² W. D. MATTHEW and W. GRANGER, "New Fossil Mammals from the Pliocene of Sze-Chuan, China", *Bull. Am. Mus. Nat. Hist.*, vol. XLVIII, 1923, p. 594.

³ Owing to the kindness of Mr. M. A. HINTON, I have been able to examine at leisure the large collection of recent Suid skulls in the British Museum. There are only three pig skulls from China in this collection: one from Shansi, one labelled *Sus moupinensis* MILNE EDWARDS from the Sze-Chuan mountains of Southern China, and a larger one, labelled *Sus leucomystax*, from Shanghai. On these I have based my comparisons.

In 1917 SOWERBY¹ published an account of his critical examination of the material in the Sikawei Museum in Shanghai. Here were the thirty recent skulls of *Sus* out of which the Jesuit Père Heude, in his "Mémoires concernant l'Histoire Naturelle de l'Empire Chinois" had made eighteen species, although they came from only thirteen different localities. SOWERBY found no grounds for distinguishing more than five species, coming from five different regions and differing from one another in size and proportions. He recognised that there was considerable individual variation among the pigs within each of these regions, a variation which his own hunting experience had taught him to expect. Of the skulls from the Yang-tze valley, out of which Heude had made some seven species, he says: "I should not hesitate to class them as one species, with the note that the specimens from Kienté district (Poyang Lake District), where the feeding is probably good and plentiful, are somewhat larger than those from further east (i. e. Chinkiang and Ningfou districts)."

SOWERBY gives no comparative measurements of his five species, and indeed nothing less than a series of twenty or twenty-five skulls of each of them, to give some idea of the range of individual variation, would make such measurements of any real value. Nor does he mention any morphological differences. It is thus impossible to estimate the probable nearness of relationship between the pigs of the loess and the pigs living in the same or other districts in China today, or, admitting an ancestral relationship, to measure the amount of evolutionary change, if any, that has taken place since Pleistocene times. In other words, it is not possible, with the material available, to establish the existences of differences of specific or evolutionary significance between the loess pigs and the recent pigs. The former, like the latter, show considerable variation in size but no obvious morphological differences.

The following is a list of the Pleistocene material in the *Lagrelius* collection, (localities 105, 106, 67, 61):

1. Fragment of snout from locality 105, (typical loess of southernmost Shansi) (Pl. I, fig. 1). P^1 to m^3 of the left side, and p^2 to m^3 of the right side are in place and well worn. There is a short diastema of 3.8 mm. between p^1 and p^2 . The talon of p^3 is prominent, though rather less so than in the recent skulls in the British Museum; the talon of p^2 is very small. The infra-orbital foramen lies above the anterior roots of m^1 . The posterior palatine foramina are at the level of the anterior roots of m^3 . At the anterior end of the zygoma the depression for the origin of the *depressor*

¹ A. DE C. SOWERBY, "On Heude's Collection of Pigs, Sika, Serows and Gorals in the Sikawei Museum, Shanghai". Proc. Zool. Soc. Lond. 1917, p. 7.

rostri muscle, and the ridge above it for the *dilatator naris* muscle, are well developed; above these the depression for the *levator rostri* muscle is also deep.

Length from p^2 to m^3 inclusive	108 mm.
" " p^3 to m^3 " 	96 mm.
Breadth of palate at antero-internal roots of m^3	38.6 mm.
LM ¹ —	BM ¹ 15.4 mm.
LM ² 22.2 mm.	BM ² 19.7 mm. (left), 20.0 mm. (right)
LM ³ 35.3 mm.	BM ³ 21.6 mm. (left), 22.0 mm. (right)

2. Also from locality 105 come a number of isolated teeth apparently all belonging to the same species as (1) above.

a) An associated right m^2 and m^3 , larger than those of (1) above, (text-fig. 35 a).

LM ² 23.8 mm.	BM ² 21.0 mm.
LM ³ 37.5 mm.	BM ³ 23.7 mm.

b) A well worn m^1 , also larger than that of (1) above.

LM ¹ 17.1 mm.	BM ¹ —
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c) A left p^3 , a right p^2 , and a left p_1 .

d) The well worn crown of a very stout male right upper canine, (text-fig. 35 c). The enamel is restricted, in the typical *Sus* fashion, to a broader band on the ventral surface and a very narrow band postero-dorsally.

e) A female right upper canine, less than half the thickness of the male canine and two-rooted. It is worn almost to the base of the broader enamel band, (text-fig. 35 b).

f) A pair of female lower canines, well worn on both the hinder and anterior surfaces, (text-fig. 35 d).

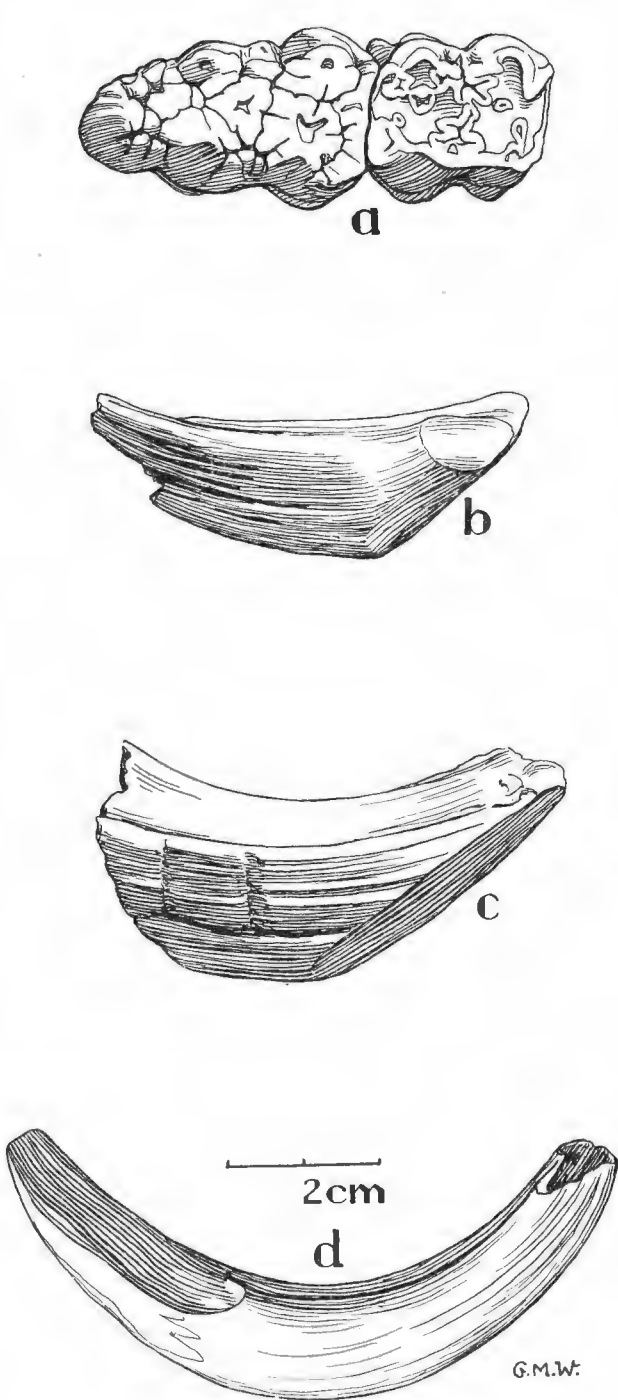
g) A left and right i_2 , and a left i_1 .

h) A small fragment of a right mandible with broken talonid of m_3 .

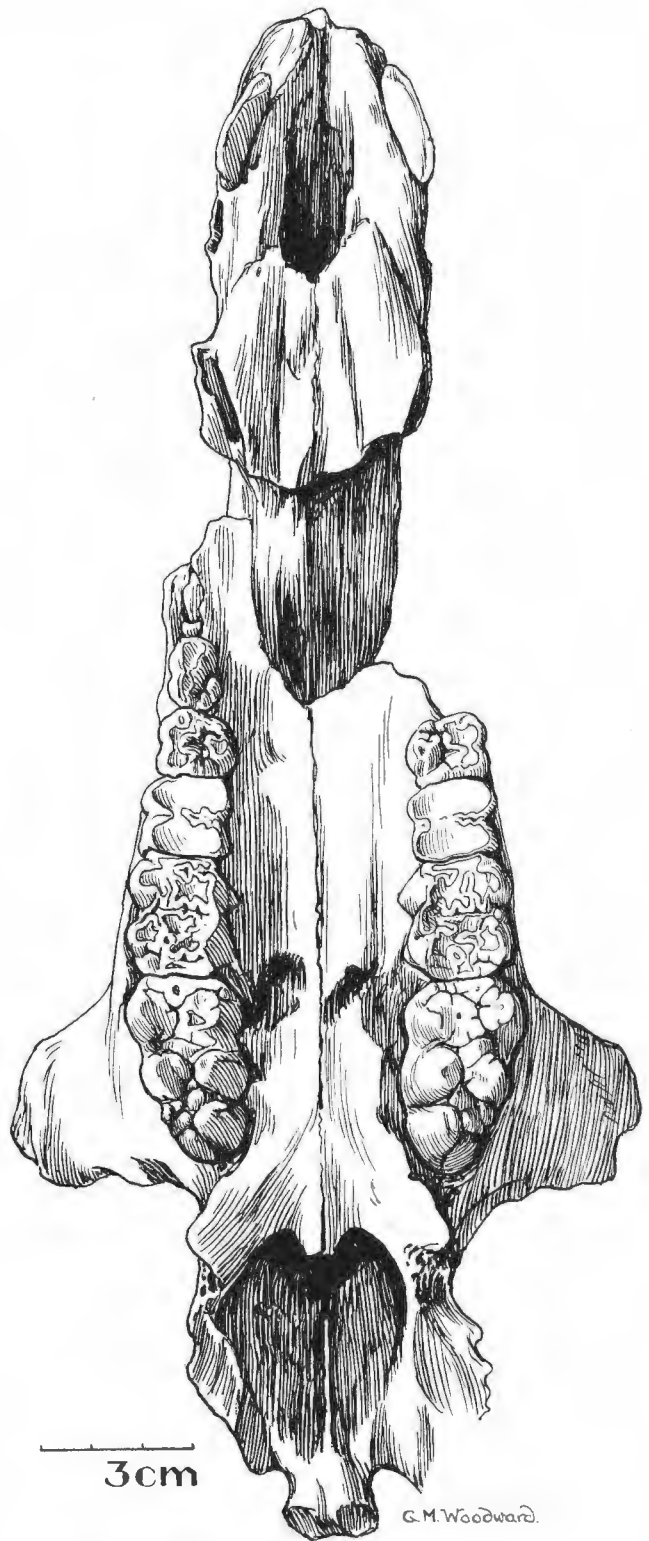
i) A number of phalanges.

3. From locality 106, likewise typical loess in southernmost Shansi, come the posterior end of an m^3 and a right and left i_3 .

4. The broken anterior end of a skull from locality 67 in Chihli (text-fig. 36). The second upper incisors are alone present of the anterior teeth; of the cheek teeth p^3 to m^3 on the left side, and p^4 to m^3 on the right. The low crowns of the second incisors are extremely long in antero-posterior dimension, but this length is a very variable one in recent pigs and may here be an individual peculiarity. The cheek



Text-fig. 35. *Sus sp.* Isolated teeth from typical loess of Southernmost Shansi (loc. 105) Natural size. a) Right m^2 and m^1 . b) Right upper canine of female, ventral view, showing remains of ventral enamel band. c) Fragment of right upper canine of male, ventral view, showing ventral enamel band. d) Right lower canine of female, postero-lingual view.



Text-fig. 36. *Sus sp.* Anterior end of skull from loc. 67 in Chihli. Two thirds natural size.

The other fragment from deposits probably subsequent to the loess is also of a smaller animal than the typical loess pigs so far collected; it is comparable in size with the British Museum skull from the Sze-Chuen mountains, and comes from Nan-Shan in the Hsuan-Hua-Hsien district of Chihli. It consists of two broken halves of a mandible with their lower canines, p_3 to m_2 on the left side, p_4 to m_3 on the right; all the teeth are so very worn and in such very poor condition that little can be learnt from them.

LM ₁ 15.0 mm.	BM ₁ —
LM ₂ 21.6 mm.	BM ₂ 15.4 mm.
LM ₃ 35.4 mm.	BM ₃ 17.9 mm.

[Since writing the above account of the Pleistocene Suidæ in the *Lagrelius* collection, I have received from Professor WIMAN two fragments of a mandible from Hung-Kou in the Hsin-An-Hsien district of Honan. Professor ZDANSKY writes to me that he thinks the Pleistocene age of this specimen can hardly be doubted, both from its mode of preservation and from its similarity to the pigs from the Pleistocene cave fauna of Chou-K'ou-Tien. He proposes to name these pigs *Sus Lydekkeri*.¹

In the present specimen m_3 is the only tooth sufficiently well preserved to comment upon. It agrees quite well with the m_3 from locality 61 referred to above, but is longer. Noteworthy is the way in which the talonid bears a pair of large opposite cusps which in size and relations closely match the pairs on the anterior and middle lobes of the tooth, thus giving the tooth an almost trilophodont appearance; this is probably merely an individual peculiarity.]

Discussion.

1. The Relationships of the Chinese *Sus*.

As stated above, the Pleistocene *Sus* of Northern China appears from its dentition to be closely related to the races living in China today, but in order to substantiate this more material of both living and extinct forms is needed.

In dental characters the three recent Chinese skulls in the British Museum (see footnote p. 62) are barely distinguishable on the one hand from those of the Japanese pigs usually known as *Sus leucomystax* and on the other hand from the pigs of

¹ O. ZDANSKY. "Die Säugethiere der Quartärfauna von Chou-K'ou-Tien". Pal. Sin. Ser. C. 1927. Vol. 5. pp. 91—101.

Prof. ZDANSKY has kindly allowed me to examine the Chou-K'ou-Tien material described by him. A number of individuals are represented, often only by isolated teeth. The average size appears to have been larger than that of the individuals from the loess and loc. 67, but I can find no characters that definitely call for specific distinction.

Siam and Annam to the south. These latter bear the museum label *Sus cristatus*, but in their turn grade by almost imperceptible differences into the pigs of the Malay peninsula, and these into the typical *Sus vittatus* of Sumatra. This series is readily distinguishable from the races of *Sus cristatus* living in Central India and Malabar by the greater simplicity of the cheek teeth and shorter last molars, but the pigs to the north of India, in Nepal and Sikkim, appear to be intermediate in character between those of southern India and those from China. Such a distribution of relationships is very similar to that which MORANT has shown to exist among the Oriental races of Man.¹ To draw up any reliable scheme of relationships it would, however, be necessary to use statistical methods such as those employed by MORANT; but these methods are of little value unless at least thirty skulls of each race are available, which is rarely the case in our museums.

The need for more material was strongly emphasised by FORSYTH MAJOR as long ago as 1883.² He pointed out then how the numerous living races of *Sus* are separated from one another by extremely small differences of no very constant character. In order to make sure of these differences it is necessary to take a large number of pigs from each locality and to consider as large a number of characters as possible. A single individual may in some of its characters resemble the pigs from another locality, or at any rate be intermediate between them and the average member of its own community. In continental areas the nearer two communities are to one another the more nearly they resemble each other, the differences between neighbouring communities being almost imperceptible. In this way one race of pigs grades into another throughout the whole of the Palæarctic and Oriental regions.

FORSYTH MAJOR believed that when recent Chinese pigs were better known they would prove to be intermediate in type between the Oriental races to the south of them and *Sus scrofa*. A comparison of a single skull from the Tien-Shan mountains on the western borders of Chinese Turkestan (*Sus nigripes*, No. 12. 7. 27. 1, in the British Museum) with those from the east of China on the one hand and those from eastern Europe and Asia Minor on the other hand (*Sus attila*, *Sus lybicus*), to some

¹ G. M. MORANT, "A Study of Certain Oriental Series of Crania Including the Nepalese and Tibetan Series in the British Museum (Natural History), *Biometrika*, Vol. XVI. 1924, p. 1.

P: 47. "A comparison of the skull measurements of seven of the principal races of India and the Orient has shown that they may be arranged in a series such that adjacent members are intimately related while the extremes are of markedly divergent types."

² C. T. FORSYTH MAJOR, "Studien zur Geschichte der Wildschweine (Gen. Sus)." *Zool. Anzeiger*, VI. 1883, p. 295.

That FORSYTH MAJOR felt the need for some statistical method of attacking this type of biological problem is evident from a paper of his entitled: "I Cinghiali dell' Italia. Studi craniologici", (*Atti della soc. Toscana di scienze naturali-Pisa*. Vol. VI. fasc. 2. 1885. P. 346).

extent bears this out, but the material is still far too inadequate to base any real conclusions upon.

In FORSYTH MAJOR'S opinion *Sus vittatus* of the Malay Peninsula, Sumatra, etc., represents the remains of a once widespread primitive type, while the Oriental *S. cristatus* is its immediate derivative and successor, and the Palæartic *Sus scrofa* the most modern representative of the series. He claimed that no hard and fast line could be drawn between any of these species: each type had been derived in turn from the other by a continuous process of evolution and each is nowadays still in geographical continuity with the other.

2. *Propotamochoærus hyotherioides*, and Pilgrim's theory of the diphyletic evolution of the Suidæ.

The evidence of the palæontological record as to the primitive nature of *Sus vittatus* is not clear. Until PILGRIM'S recent work on the Indian fossil Suidæ,¹ little new has been added to our knowledge of the Old World fossil forms since STEHLIN'S comprehensive monograph of 1898.² PILGRIM has considerably increased our knowledge of the Indian Suidæ, and clarified our ideas about them, but it is doubtful whether the great phylogenetic scheme which he has drawn up for the whole family will not have to be fundamentally modified if the gaps in our knowledge of early Tertiary Suidæ are ever filled. Moreover, many of the very numerous species which PILGRIM introduces into his scheme are created out of material which is fragmentary in the extreme and which hardly justifies such a detailed and elaborate phylogeny as he has ventured upon.

The main difference between PILGRIM'S views as to the evolution of the Suidæ and those put forward by STEHLIN in 1898 is the former's claim for a division of the family into two phyla, each with a totally separate development since the Lower Eocene. One of these phyla is represented today by *Potamochoærus*, the other by *Sus*. PILGRIM bases this division almost entirely on the character of p_4 . In *Potamochoærus* the main cusp of this tooth is a simple unsplit cone with steep anterior face, whereas in *Sus* the central part of the tooth is incompletely cleft into twin summits, the one almost but not quite behind the other, while the anterior part is raised so as to be nearly as high as the central part. STEHLIN believed that both *Sus* and *Potamochoærus* took origin from some such form as the Pontian *Sus palæochoærus*, where

¹ G. E. PILGRIM, "The Fossil Suidæ of India", N. S. Vol. VIII. 1926. Memoir No. 4.

² H. G. STEHLIN, "Geschichte des Suiden-Gebisses", Abh. d. Schweiz. pal. Gesell., vols. XXVI—XXVII, 1899—1900.

p_4 is like that of the earlier Miocene *Hyotherium Sæmmeringii* and the Oligocene *Palæochærus*; in these three fossil forms, which he believed to be a phyletic series, p_4 is very distinctly cleft into twin summits, and these stand side by side, the one only a little posterior to the other, while the anterior end of the tooth is not yet raised though the contour is not quite so steep as in *Potamochærus*.

PILGRIM, however, claims that the *Potamochærus* type of p_4 is to be found in Indian deposits as early as the Tortonian, in his genus *Propotamochærus*, and that it had common origin with the *Hyotherium simorrense* type (his new genus *Conohyus*), which is to be found in India contemporary with it and which, except for an enlargement of the premolars, very strongly resembles it. This view as to the near relationship of *Propotamochærus* and *Hyotherium simorrense* may be the correct one, but to the present writer PILGRIM, in his diphyletic pedigree, appears to have laid too much weight on the cleft or uncleft nature of the main cusp of p_4 . The following reasons seem to weaken his general argument:

a) The presence of an uncleft p_4 in the Upper Eocene genera *Cebochærus*, *Chæromorus* and *Chæropotamus* is no proof that p_4 was of this type in the Upper Eocene Suidæ, because, as I have elsewhere tried to show,¹ these genera were not Suidæ at all: *Propalæochærus* and *Doliochærus*, both with cleft p_4 , are the earliest Suidæ as yet known to us. Furthermore the Middle Miocene *Chærotherium* is not, as PILGRIM has assumed, a member of the true Suinæ, the sub-family with which we are here concerned.²

b) It is unlikely that a single, very small character of this type should have remained constantly different since the Upper Eocene in two lines of Suidæ so closely parallel in all other characters, and each giving rise to so many very similar offshoots.³

c) The character is not a constant one, even in those genera which PILGRIM refers with most confidence to one or other of his phyla. Thus, as STEHLIN has pointed out, faint traces of a posterior peak may sometimes be found on the main cusp of p_4 in *Potamochærus*, while PILGRIM himself admits that similar traces may be found both

¹ H. S. PEARSON "On the skulls of Early Tertiary Suidæ — — —". Phil. Trans. Roy. Soc. Lond., ser. B. vol. 215, 1927. pp. 412—414, and p. 435.

² Ibid. pp. 405—410.

³ A year later than his monograph of 1926, in a paper entitled "The Lower Canine of Tetraconodon" (Rec. Geol. Surv. Ind. LX. 1927, p. 160.) PILGRIM inclines to place the separation point of his different lines of Suidæ at a rather later date, but still not later than the Lower Oligocene.

The present writer is not convinced that the possession of a verrucose canine necessarily denotes in all cases the retention of a primitive character, even though it is the retention of a youthful character and is found in the females of all races throughout life. The occurrence of such a canine in the males of any race might just as well be a sign of secondary weakness and degeneration in this organ; this was Stehlin's view as to the canines of *Microstonyx* (Geschichte des Suiden-Gebisses, p. 251).

in his Indian *Propotamochærus* and in *Hyotherium simorreense*. Some skulls of *Sus vittatus*, on the other hand, have the two peaks usually present in *Sus* so closely approximated as to give the effect of a single projection, and all trace of separation is lost if the tooth be ever so slightly worn. Already in this paper I have drawn attention to a similar case in *Chleuastochærus* (p. 29 and 30) STEHLIN found extreme difficulty in deciding whether the premolars of certain European Lower Pliocene species were nearer to *Potamochærus* or to *Sus*.¹

The same difficulty arises in the case of the Chinese material described above as *Propotamochærus hyotherioides*. In general character the dentition is extremely similar to that of PILGRIM's Indian *Propotamochærus* and of "*Sus*" (*Propotamochærus*) *provincialis* of the European Plaisancian (Montpellier). That is to say the teeth are of a robust type with thick enamel and with the primitive ground pattern of the cusps unobscured by the addition of many accessory folds and cusplets. P^2 , p^3 and p_3 are long teeth. In p^2 and p^3 there is no complete internal cingulum, but an anterior cingulum and a well developed postero-internal talon. In p_4 the anterior slope of the main cusp is a very abrupt one, the anterior cingulum very slight, and the posterior end of the tooth (or talonid) not nearly as high as the main cusp when the latter is unworn; by these characters of p_4 it can at once be distinguished from species such as *Sus Strozzi* of the Val d'Arno, which have a similar robust, simple type of dentition, but in which the anterior end of p_4 is already partially elevated, (see STEHLIN, loc. cit. Pl. III. figs. 1 to 5).

Although there is thus every reason for regarding the Chinese species as of the same genus as those from India and Montpellier, there is nevertheless difficulty in naming it *Propotamochærus* since PILGRIM has defined that genus as possessing an uncleft or very indistinctly cleft p_4 . In *Propotamochærus hyotherioides* p_4 has a main cusp as clearly cleft as in some species of *Sus*.

3. Increased complexity in progressive races, reduction in unprogressive races of Suidæ.

If the recent *Potamochærus* is derived from *Propotamochærus* of the Pliocene its premolar dentition has become much simplified and reduced; p^1 and p_1 are generally but not invariably lost, sometimes p_2 in addition; p^2 and p^3 have become short and peg-like, p^2 usually losing its talon, which in p^3 is reduced; the outer cusps of p^4 are approximated. It would seem as if the uncleft conical main cusp of p_4 were a

¹ H. G. STEHLIN, "Geschichte des Suiden-Gebisses", pp. 151, 152.

result of the same process of simplification. A somewhat similar tendency appears to characterise *Sus vittatus*; here also the anterior premolars are shortened and in p^2 and p^3 the internal cingula are but feebly developed, that of p^3 hardly forming a talon; and here also, as already remarked, the twin summits of p_4 are so closely approximated as to be sometimes barely distinguishable.

In both cases there is a marked contrast with races such as the typical *Sus scrofa* of Eastern Europe (*Sus scrofa attila*). In the latter p^2 and p^3 are both long teeth; p^3 has a very broad talon and also a well marked antero-internal cingulum, p^2 is almost as long and almost as complex as p^3 but more compressed. In the absence of premolar reduction such races appear to be primitive, but on the other hand their teeth have lost the primitive robustness and simple pattern. *Potamochoerus* and *Sus vittatus* have retained these latter characters but their premolars have undergone reduction.

It appears that a tendency towards premolar reduction is a common one among southern races of Suidæ. It has occurred independently, but by very similar methods, in *Sus vittatus* and in *Potamochoerus*: in *Babirussa*, which probably branched off from the main stock at least as early as the latter; in the Ethiopian *Hylochoerus*, where the reduction is very far advanced; in *Phacochoerus*,¹ where it has reached an extreme; lastly, in a peculiar small species from the Pleistocene breccia of Sardinia, fragments of which, showing an extreme reduction of the premolars, were recently shown me by Dr. Stehlin in Basel.

It is thus not possible to accept in their entirety FORSYTH MAJOR'S views as to the primitive nature of *Sus vittatus*. His conclusions were based on comparisons of the shape and proportions of the skull. He claimed that the fundamental characters of the *Sus vittatus* skull are such as appear in youthful skulls of *Sus scrofa*, and that amongst fossil forms the *Sus scrofa* characteristics become less evident the older geologically these fossils are, making way for forms that first of all approach *Sus vittatus*, then *Sus verrucosus*, finally *Potamochoerus*. In studying the British Museum collection of recent Suidæ the present writer has concentrated on the premolar differences, as it is these which STEHLIN and PILGRIM have found of most use for distinguishing fossil forms. It seems probable, however, that some at any rate of the characters which FORSYTH MAJOR regarded as primitive in the skull of *Sus vittatus* may be directly or indirectly correlated with the reduction in dentition, this leading to a shortening of the jaws and consequent need for readjustments throughout the skull.

¹ In *Hylochoerus* and *Phacochoerus* this reduction of the premolars is accompanied by an increase in importance of the molars, but in the other races the molars remain very simple, short and primitive. It would be interesting to know whether the food of these latter is on the whole of a softer nature than that of the northern races.

Thus a careful analysis would probably show that in the skull as in the dentition of *Sus vittatus* Pliocene characters are mingled with others more recently acquired. *Potamochoerus* has retained characters which date back to an even earlier period in the history of the Suidæ, but at the same time has undergone a still greater reduction in dentition, while its skull has acquired peculiarities known in no other branch of the family. The *Sus scrofa* races of Eastern Europe may probably be regarded as the most progressive among the Suidæ today:¹ that is to say they exhibit the most novel and up-to-date character without having suffered any great reduction of parts. The races of India, partly intermediate in character between *S. vittatus* and *S. scrofa*, partly showing incipient specialisations of their own², probably split off from the main stock at a considerably later date than the former, the Chinese races at only a slightly later date.

The relationships of the different races of the Malay Archipelago are much too complex to be considered here. The typical Javan *S. verrucosus* cannot be regarded as the first term in the *Sus-vittatus-cristatus-scrofa* series, as Forsyth Major was inclined to regard it, for its premolars are of sectorial type, showing no signs of reduction. P² and p₃ are long teeth. The internal cingulum of p² and p³ forms a well-marked, low, inner crest to the tooth, completely separated from the base of the main cusp along its whole length. The lower premolars are compressed teeth with very high talonids, the twin cusps on p₄ nearly one behind the other. These premolar characters can be derived most easily direct from those of *Hyotherium Sæmmeringii* through some Pontian form such as *Sus palæochærus*. PILGRIM has also suggested a relationship to the Indian Dhok Pathan zone *S. præcox* (known only as isolated teeth). Why this Javan form alone among the southern races should have retained sectorial premolars it is hard to say. Interesting is the possession by most, though not all, skulls of this species of a pair of depressions in the pterygoid region, on the roof of the nasopharyngeal canal; similar depressions are generally present in two such widely different types as *Babirussa* and *Phacochoerus*, types which probably also split off at an early date from the main stock of the Suidæ.

4. *Microstonyx erymanthius* and *Dicoryphochærus* PILGRIM.

That *Microstonyx erymanthius*, or a closely allied species, should be found in the Chinese *Hipparion* fauna is no more than might be expected in view of the many other elements which that fauna has in common with the Pikermi fauna. If however, the

¹ No skulls from Western Europe and Northern Asia were available to the present writer, however.

² As, for instance, the long and complex third molars in some but not all of these races.

shortness of the symphysis of the mandible from locality 114 was really characteristic of the living animal, and is not due to impaction of the bone after death, it is possible that the relationships of this large Chinese pig are with the Indian pigs which PILGRIM has named collectively *Dicoryphochærus* rather than with the Pikermi *Microstonyx*. Unlike the latter, the males of these Indian forms have large canines, but the females appear to agree with *Microstonyx* in all characters except the shorter symphysis. In a general way PILGRIM'S earlier stages of *Dicoryphochærus* (*D. instabilis*, *haydeni*, *chisholmi* of the Chinji zone) seem to lead on through the later stages (*D. vagus*, *vinayaki*, etc. of the Dhok Pathan zone) more or less directly into *Sus*: among other changes in the dentition, p_4 becomes a more compressed sectorial tooth, its deutoconid gradually shifting backwards into line with its protoconid, while the posterior end of the tooth becomes gradually elevated. It was probably before the end of the *Dicoryphochærus* phase that there branched off from the main line the phylum of which *Sus vittatus* is the present day representative. If PILGRIM'S correlation of the Siwalik horizons be correct, *Microstonyx* must be regarded as collateral with *Dicoryphochærus* and very closely allied to it.

5. *Chleuastochærus*.

Chleuastochærus appears to have been the only type of pig that was at all common in the Chinese *Hipparion* fauna, and it has hitherto never been found elsewhere¹. The abundance of this little, rather peculiar form, and the scarcity of types such as *Propotamochærus* and *Microstonyx* which are characteristic of contemporary or nearly contemporary faunæ elsewhere, and which are more or less closely allied to the dominant genera of today, may perhaps indicate a difference of facies. It has been tentatively suggested by RINGSTRÖM and others that steppe conditions prevailed in China during Pontian times. If so, it is possible that *Chleuastochærus* was a form in some way more especially adapted to the open life of the steppes, whereas the two larger genera inhabited the neighbouring wooded land, or the rare "wood islands", and only occasionally wandered out and mingled with the true steppe fauna.² The precocious reduction of the lateral digits of *Chleuastochærus*, compared with those in most recent Suinæ, does not necessarily lend support to the steppe theory however,

¹ Unless some of the rare Indian teeth referred by PILGRIM to *Palæochærus* belonged in reality to a species of *Chleuastochærus*.

² A. NEHRING, in his "Ueber Tundren und Steppen der Jetzt- und Vorzeit", quotes from the accounts of various writers who mention the modern *Sus scrofa ferox* as one of the animals which, though not a "Charakterthier" of the South Russian and Volgo-Uralian steppes, was formerly nevertheless a frequent visitor.

since an even greater reduction has taken place in the New World genus *Dicotyles*, although this is apparently as much a forest form as *Sus*.

All that can be said about this small Chinese genus is that, mingling as it does certain rather grotesque with other very primitive characters, it appears to have been the terminal form of a special little line of evolution of its own of whose Miocene stages we know nothing, but which we must derive, quite independently of the European Miocene *Hyotherium*, from some Oligocene species that would almost certainly have fallen within the genus *Palæochærus*.

Summary of Relationships of Chinese Fossil Suidæ.

Listriodon gigas sp. nov. (Not later than the Pontian nor earlier than the Middle Miocene).

Giant terminal form of otherwise unknown phylum. Nearest known relatives, the small bunodont species of *Listriodon* from the early Miocene of Europe and India.

Chleuastochærus Stehlini SCHLOSSER. (Pontian).

Peculiar terminal form of otherwise unknown phylum. Nearest known relatives certain species of *Palæochærus* from the European Oligocene.

Microstonyx cfr. *erymanthius* ROTH and WAGNER? (Pontian).

Relationships cannot be certainly determined without more material. They may lie either with the contemporary *Microstonyx erymanthius* of Pikermi, or with the earlier (Chinji zone) species of the Indian phylum named by PILGRIM *Dicoryphochærus* — i. e. with what is probably the ancestral line of the true *Sus*, — or they may be intermediate between the two.

Propotamochærus hyotherioides SCHLOSSER. (Pontian — and later?)

Closely related to the *Propotamochærus* species of India (claimed by PILGRIM to have existed as early as the Tortonian) and to those of the European Plaisancian.

Sus sp. (Pleistocene and later).

Closely similar to the modern Chinese *Sus* and to the Japanese *S. leucomystax*, which hold a central position between the more primitive Malayan *S. vittatus* and the more progressive European *S. scrofa*.

EXPLANATION TO THE PLATES.

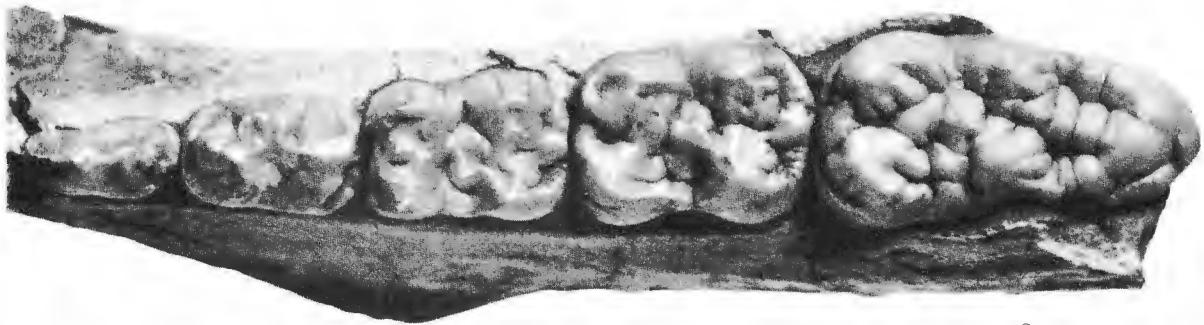
PLATE I.

PLATE I.

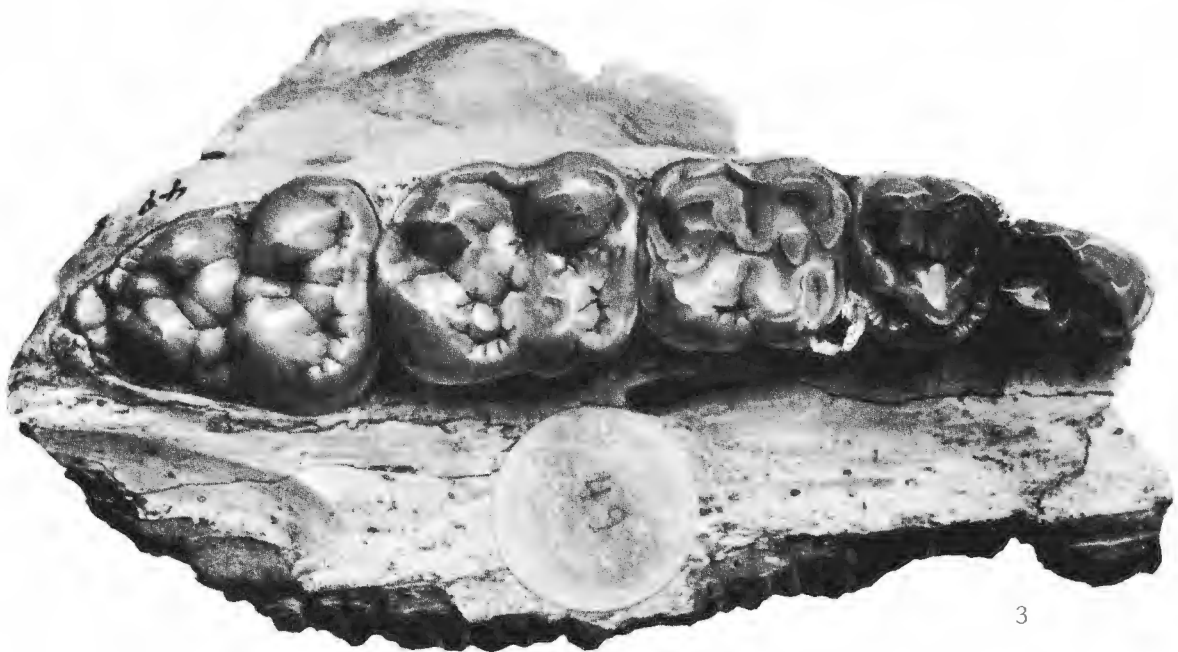
- Fig. 1. *Sus sp.* Left p^1 to m^3 from loc. 105 (typical loess). $\times 1$ p. 63
,, 2. *Chleuastochærus Stehlini* gen. nov., sp. SCHLOSSER. Left p_3 to m_3 from
loc. 49. $\times 2$. (Part of same male mandible as shown in text-figs. 19
and 22) ,, 29
,, 3. *Chleuastochærus Stehlini*. Right p^3 to m^3 from loc. 49. $\times 2$,, 29



1



2



3

PLATE II.

PLATE II.

- Fig. 1. *Chleuastochærus Stehlini* gen. nov., sp. SCHLOSSER. Left p^3 to m^2 from loc. 49. $\times 2$. In this specimen the two external cusps of p^4 are almost confluent..... p. 29
- „ 2. The same, lingual view.
- „ 3. *Chleuastochærus Stehlini*. Right p^4 to m^2 from loc. 30₂. $\times 2$. In p_4 of this specimen protoconid and deutoconid are almost confluent. External view „ 30
- „ 4. The same, crown view.



1



2



3

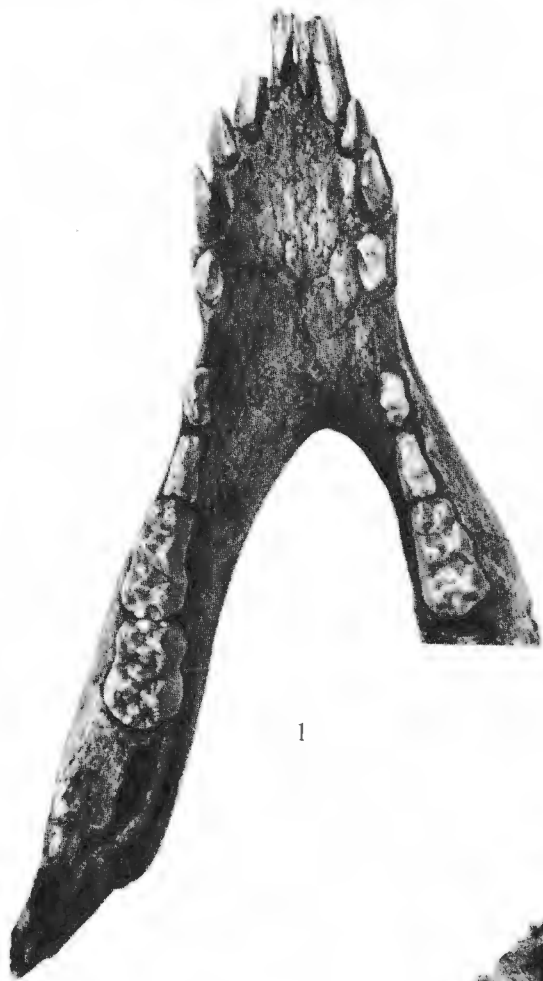


4

PLATE III.

PLATE III.

- Fig. 1. *Chleuastochærus Stehlini* gen. nov., sp. SCHLOSSER. Mandible of young individual with milk dentition, from loc. 49. × 1. p. 27
- „ 2. *Chleuastochærus Stehlini*. Skull fragment of young individual with dm^2 to m^1 , from loc. 49. × 1 „ 27
- „ 3. *Microstonyx erymanthius* ROTH and WAGNER? Right dm_2 to m_1 , from loc. 114 north. × 1 „ 52
- „ 4. The same, external view.



1



2



3

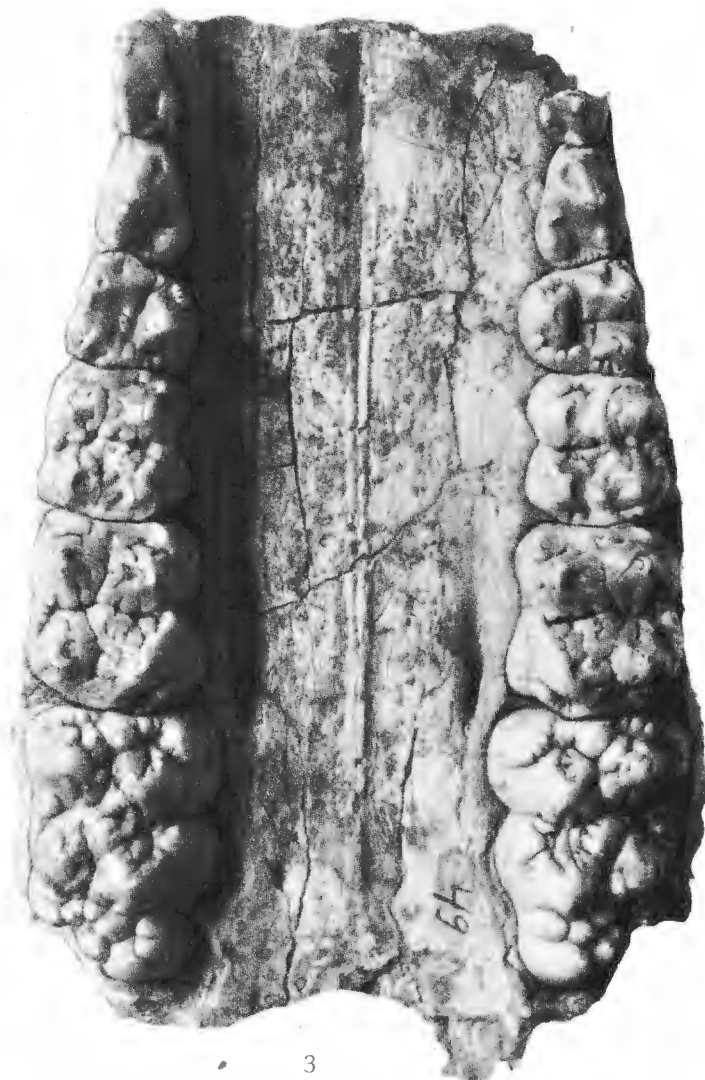
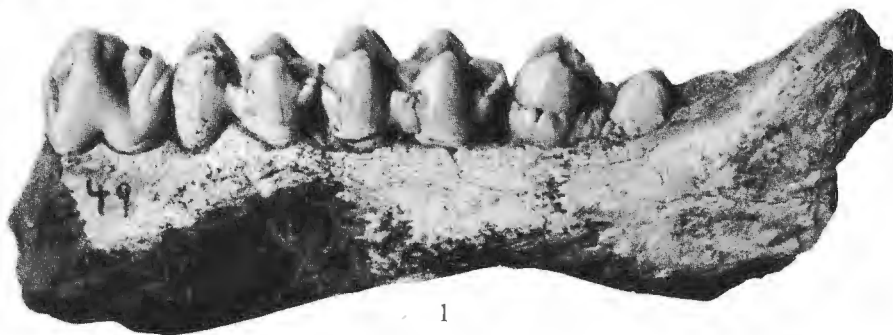


4

PLATE IV.

PLATE IV.

- Fig. 1. *Propotamochærus hyotherioides* SCHLOSSER. Left p_4 to m_2 from loc. 49.
× 1. External view p. 58
„ 2. The same, crown view.
„ 3. *Propotamochærus hyotherioides*. Palate from loc. 49. × 1 „ 58



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BY

HELGA SHARPE PEARSON
UNIVERSITY COLLEGE, LONDON

PLATES I-IV AND 37 TEXT-FIGURES



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